5-1996

The Influence of Forest Fragmentation and Landscape Pattern on American Martens and Their Prey

Christina D. Hargis
Utah State University

THE INFLUENCE OF FOREST FRAGMENTATION AND LANDSCAPE PATTERN ON AMERICAN MARTENS AND THEIR PREY

by

Christina D. Hargis

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Fisheries and Wildlife

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1996

ABSTRACT

The Influence of Forest Fragmentation and Landscape Pattern

on American Martens and Their Prey

by

Christina D. Hargis, Doctor of Philosophy

Utah State University, 1996

Major Professor: Dr. John A. Bissonette
Department: Fisheries and Wildlife

Habitat fragmentation occurs when large tracts of an orginal habitat are replaced by smaller patches of two or more habitat types, largely through human activities. I studied the behavior of six measures of landscape pattern that seemed appropriate for quantifying fragmentation, and used these measures to investigate the effects of forest fragmentation on American martens (*Martes americana*) and their prey. The measures I selected were edge density, contagion, mean nearest neighbor distance between patches, mean proximity index, perimeter-area fractal dimension, and mass fractal dimension. To test the behavior of these measures with a variety of landscape patterns, I used a computer program to create nine series of increasingly fragmented landscapes that differed in the size and shape of patches, and in the way fragmentation was allowed to increase.

Patch size changed the range of attainable values for all measures examined, and patch shape affected all measures except nearest neighbor distance and mean proximity

index. The method in which fragmentation increased within each landscape series also affected all measures. None of the measures was able to differentiate between different spatial distributions of patches.

To investigate the effects of forest fragmentation on martens and their prey, I selected 18 areas of mature forest habitat in Utah that differed in the amount of landscape heterogeneity due to natural openings and timber clearcuts. I conducted a live-trap survey of martens within each site over three summers from 1991-1993, and a 7-week snap-trap survey of small mammals within 12 of the sites in 1992.

Martens were negatively correlated with increasing fragmentation, and mean proximity index was the strongest correlate with reductions in marten captures across sites ($\chi^2 = 9.48$, df = 1, $P = 0.04$). Capture rates of red-backed voles (*Clethrionomys gapperi*) also declined with increasing fragmentation ($\chi^2 = 4.66$, df = 1, $P = 0.03$), while deer mice (*Peromyscus maniculatus*) capture rates increased ($\chi^2 = 6.12$, df = 1, $P = 0.01$). Martens and voles both appeared sensitive to landscape pattern, with low numbers in areas having large, closely spaced patches of unforested habitat.

(154 pages)

DEDICATION

To Mafuta

I humbly dedicate this to you and all others
whom I met too briefly in my search for knowledge

ACKNOWLEDGMENTS

It is a sincere pleasure to acknowledge those who provided me with support and inspiration during the course of my doctoral research. This project was funded by the Utah Division of Wildlife Resources, the Ashley and Wasatch-Cache National Forests, and the Utah Wilderness Association. Within the Division of Wildlife Resources, I am especially indebted to Randy Radant, who helped get the project running, and to Ken McDonald and Boyd Blackwell for the loan of snap traps and use of the Mirror Lake cabin. Within the Forest Service, Floyd Bartlett was tremendously supportive, loaning me personal equipment when Forest Service supplies were not available, and providing temporary housing for field assistants during the first summer. Kathy Paulin also was a key player, providing access to needed maps and aerial photos and sharing her knowledge of the Uinta Mountains. Other Forest Service personnel who assisted with supplies, information, and even a bit of field work were Sherel Goodrich, Wendy Reinmuth, Sara Dewey, Mary Clough, and Kent O'Dell.

I am grateful to John Bissonette, my major professor, for having faith in my abilities, and offering me a challenging and choice research opportunity. He supported and encouraged me through all aspects of my studies and research, and through him, I experienced "... that mysterious meeting in life when someone acknowledges who we are and what we can be, igniting the circuits of our highest potential" (Rusty Berkus, date unknown). As I embark in my future endeavors, I hope I will be a tribute to his mentorship.

I thank the members of my committee, Mike Conover, Mark Ritchie, Jim Long, and Doug Ramsey, for advice during the development of my research design, and for insightful and helpful reviews of dissertation drafts. I wish to express special thanks to Dave Turner, who invested numerous hours of statistical support that greatly improved the analysis of my data. Susan Durham also provided consultation and special insight into statistical methods.

I was fortunate to have the good company and energetic field assistance of the following individuals, all of whom remained amazingly cheerful under the most arduous of conditions: Ray Vinkey, Colleen Zank, Stacy Kuerner, Pete Lortz, Todd Sajwaj, Dave Masters, Alex Krawarik, Holiday Sloan, Rob Rood, and Kyle Lischak. I thank them for often going beyond the required duties to bring the highest quality and accuracy to the collected data.

I appreciate use of the FRAGSTATS spatial pattern analysis program developed by Kevin McGarigal and Barbara Marks at Oregon State University, and thank Bruce Milne and Tim Keitt, University of New Mexico, for use of their software for calculating mass fractal dimension. I also thank Bruce for his consultation on mass fractal dimension and for reviewing Chapter 2. I appreciate access to the supercomputer facility at the Albuquerque Resource Center, made available to a variety of users under sponsorship in part by the Phillips Laboratory, Air Force Materiel Command, USAF, under cooperative agreement number F29601-93-2-0001. I also acknowledge use of the KHOROS® software development environment. KHOROS® is a registered trademark of Khoral Research, Inc.

I am indebted to EBo (John David) for tremendous support and encouragement during the latter part of my research. He volunteered hundreds of hours to develop and run the computer program I needed for creating landscape simulations, making it possible for me to conduct a rigorous analysis of landscape metrics. This in itself was a major contribution, but he also gave me tremendous emotional support, meeting so many of my needs, both expressed and unspoken.

Several others have played a role in my doctoral research through the influence they have had on my life: my parents, William and Priscilla Devin, for introducing me to the mountains and teaching me to value all beings that live there; David Graber, for inspiring me to become a biologist and serving as my mentor for many years; Barbara Bedayn, for being an exemplary woman-mother-naturalist; and Goshawk, Chickaree, Black Bear, and Marten, for touching my soul. I also acknowledge Allen Stokes and David Gaines, for their extraordinary examples in living their philosophy; my children Heather and Laurel, for their faith in me, and for recognizing my efforts on their behalf by granting me an honorary Ph.D. in Motherhood; Mead Hargis, for being a terrific father, and for helping me through the dark, financial times of my last couple years; and Rosanne Higley, for being my dearest friend, greeting my sorrows with words of comfort, and doubling my moments of joy with her enthusiasm.

Lastly, thanks to Tom Robbins for interjecting humor and philosophy into a period of my life that was often too serious and scientific. In particular, I thank him for the

following insight (Jitterbug Perfume, Bantam Books 1984, pp. 29-30), which was helpful to me as I sought meaning and significance from my data:

> The burial mound was outside the city walls, in a field dotted with cow pies and large stones. The stones had been arranged geometrically in patterns that were supposed to mean something to the gods. Presumably the cow pies had fallen at random, although then, as now, the division between what is random in nature and what is purposeful is extremely difficult to determine.
>
> Christina Devin Hargis

CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

OVERVIEW

The value of habitat to wildlife is influenced by landscape pattern. Landscapes characterized by interspersion of patches provide essential habitat for species that use two or more habitat types (Whitcomb et al. 1981), but have less value for species requiring large patches of unbroken habitat during part or all of their life histories. Incremental changes in landscape pattern and in the proportional representation of cover types cause habitat values to shift, becoming more favorable for certain species and less desirable for others. Shifts in habitat value are accelerated by the process of fragmentation, in which large tracts of an original cover type are gradually broken into smaller patches of two or more cover types or seral stages through human activities (Whitcomb et al. 1981, Ripple et al. 1991).

The full range of habitat fragmentation has received little study until quite recently. Early investigations focused on one extreme of the fragmentation continuum, when the habitat of interest was reduced to isolated remnant patches within a non-habitat matrix (Harris 1984, Wilcove et al. 1986, Addicott et al. 1987). The vast majority of these studies were "before and after" or "fragmented versus unfragmented" designs that examined changes in species diversity from loss of habitat area within remnant patches. These studies did not utilize spatial measures to quantify different levels of fragmentation, because comparisons were simply between unfragmented and fragmented states and on changes in vegetation or faunal species composition within these states. Quantification, if any, focused on individual habitat patches rather than landscapes as a whole, and were

used to ascertain the size, shape, and distance between habitat patches (Whitcomb et al. 1981, Jennersten 1988, Rylands and Keuroghlian 1989, Saunders 1989, Verboom and van Apeldoorn 1990).

To a large extent, this avenue of study has continued. In these dichotomous comparisons, the species occupying a currently fragmented landscape is compared to a known or assumed species assemblage of the original, unfragmented state (Whitcomb et al. 1981, Saunders 1989) or to that of a contemporary, unfragmented region (Rosenberg and Raphael 1986, Gibson et al. 1988, Jennersten 1988, Rylands and Keuroghlian 1989, Verboom and van Apeldoorn 1990).

Recently, the concept of fragmentation has been expanded to include the entire continuum of fragmentation, including situations where the habitat of interest serves as the landscape matrix rather than taking the form of remnant patches. Simple measures of patch characteristics no longer serve to quantify fragmentation in a meaningful way, and consequently, landscape ecologists have begun to develop additional metrics to quantify the resulting landscape patterns.

Fractal geometry has provided new approaches to quantifying landscape pattern. Introduced by Mandelbrot (1983) within the field of mathematics, fractal geometry was originally adopted by landscape ecologists as a scale-invariant tool for quantifying the irregularity of patch perimeter in relation to patch area (Lovejoy 1982, Krummel et al. 1987). As the focus on fragmentation has grown to include the landscape matrix, fractal applications have also expanded. Mass fractal dimension developed for two-dimensional surfaces (Voss 1988) has been used to quantify the irregularities in landscape matrix

caused by the size and spatial arrangement of patches (Milne 1991). A further development has introduced the concept of lacunarity, the variance in fractal measurements over increasing spatial subsamples, to quantify the texture of the landscape caused by the size distribution of patches (Plotnick et al. 1993).

Other recent approaches to measuring landscape pattern have arisen from percolation theory, an offshoot of the study of phase transitions, concerned with the flow of energy or material through a porous lattice (Stauffer 1985). Percolation theory was introduced to landscape ecology as a means of predicting large-scale flows through heterogeneous landscapes, such as the spread of fire or insect outbreaks, or dispersal patterns of rare species, when movement is restricted within a subset of the landscape classes. As applied to studies of habitat fragmentation, percolation theory provides a tool for predicting the level of habitat loss at which movements and flows would be inhibited.

Another recent addition to the study of landscape pattern has been the development of contagion indices for quantifying the degree of aggregation within each landscape class. The original contagion index (O'Neill et al. 1988) was based on information theory (Shannon and Weaver 1962), and determined adjacency probabilities between two landscape classes. This index was later modified in an attempt to increase sensitivity to spatial pattern (Li and Reynolds 1993), although this was not entirely successful, as explained in Chapter 2 of this dissertation.

Subsequent to the development of contagion indices, an important link emerged between landscape contagion and percolation theory (Gardner and O'Neill 1991). The critical probability of percolation, normally fixed by the proportion of a map occupied by a

given landscape class, was found to vary according to the degree of contagion. Percolation occurs earlier on landscapes with moderately high contagion, because larger patches associated with high contagion can link together and span an entire landscape more readily than small patches. However, landscapes with extremely high contagion represented by a single, large patch are unable to percolate even if the patch occupies > 90% of the landscape, because the landscape class is so aggregated into the single patch that it is unable to span the entire landscape (Gardner and O'Neill 1991).

As landscape pattern has become more precisely defined and measured, ecologists are able to ask more specific questions regarding habitat fragmentation effects on organisms. At small scales, experimental designs can be applied by creating specific landscape patterns with the desired number of replicates. This has been effectively carried out in grassland communities, where landscapes have been explicitly designed through mowing treatments, creating desired proportions of open areas in specific landscape patterns (Collinge and Forman 1995, Diffendorfer et al. 1995) .

For larger organisms, the greater areal extent of individual movements serves as a deterrent to creating experimental designs, necessitating the use of preexisting landscape patterns. This approach is problematic, however, because variation in vegetative conditions and topography over large extents is higher than in small, researcher-designed plots, and organismal responses to fragmentation may be masked by other aspects of environmental variation. Nevertheless, it is essential to proceed with large-scale investigations, because we cannot assume that large organisms respond to fragmentation in the same manner as smaller species. Experimental model systems are sometimes an

appropriate way to extrapolate findings from one scale to another (Wiens et al. 1993). Organisms with similar life history traits may respond to habitat fragmentation in similar ways that could be predicted from allometric rules (Holling 1992). However, if crucial environmental factors exhibit nonlinear changes across scales, reliance on allometric relationships may be misleading. A particular response to habitat fragmentation may be species specific rather than scale dependent, driven by mechanisms operating at the organismal level, such as predation risk, resource availability, and competition.

Several organismal responses to increasing habitat fragmentation are possible, many of which would be manifest at the population level. Some animal populations may demonstrate a gradual increase or decline with increasing fragmentation, whereas others may show no response until a critical threshold is reached. Other populations may show positive responses to low levels of fragmentation and negative responses thereafter.

My study focused on the effects of forest fragmentation on American martens (*Martes americana*) and their potential prey. The objectives of this study were three-fold, and are presented individually in Chapters 2, 3, and 4. These objectives were 1) to investigate the behavior of landscape metrics used to quantify habitat fragmentation; 2) to determine the effects of forest fragmentation on populations of American martens; and 3) to determine whether forest fragmentation also effects populations of small mammals that are potential prey of martens.

Chapter 2 examines landscape metrics used to quantify fragmentation, and demonstrates the expected values of these metrics when applied to a variety of simulated landscape patterns. Most landscape metrics have been developed in the last decade, and

the general behavior and theoretical limits of each measure have been determined largely through the use of mathematical proofs and applications to maps constructed from the random placement of pixels. It generally has been assumed that values for actual landscapes would be similar to those found on random pixel maps. However, actual landscapes are the result of ecological processes that constrain the size, shape, and placement of disturbance patches, and these constraints could affect the range of values attainable for each of the measures.

I supervised the development of a computer program that simulated landscapes created by ecological and anthropogenic factors. The findings presented in Chapter 2 are derived from an analysis of six landscape metrics applied to simulated landscapes that cover the full range of fragmentation while controlling for the size, shape, and placement of disturbance patches.

Chapter 3 examines the effects of forest fragmentation on populations of the American marten, using measures discussed in Chapter 2. The American marten, a carnivorous mammal associated with mature forest systems, is an example of a species that appears sensitive to forest fragmentation, as evidenced by population declines in landscapes fragmented by clearcut timber harvests (Soutiere 1979, Snyder and Bissonette 1987, Thompson and Harestad 1994). Martens avoid clearcuts and other large, open areas, especially in the winter (Soutiere 1979, Clark and Campbell 1979, Steventon and Major 1982, Hargis and McCullough 1984). This avoidance behavior has been substantiated with baitbox experiments (Drew 1995).

Although martens avoid open areas, population responses to gradual increases in

fragmentation are not well known. Studies to date have focused on fixed levels of habitat loss, based on fragmentation found within each prescribed study area (Soutiere 1979, Snyder and Bissonette 1987, Thompson and Colgan 1994). My study was designed to investigate marten population responses across a fuller range of forest fragmentation, using a series of 18 landscapes of suitable marten habitat that differed in the amount of landscape heterogeneity due to natural open areas and clearcut harvest blocks.

I predicted three possible responses of martens to increasing levels of habitat fragmentation: 1) a linear, negative decline; 2) an initial positive response, followed by a decline; and 3) an exponential, negative response. The first predicted response assumes that each increment of forest fragmentation represents a unit of habitat loss, and that if marten populations respond to fragmentation, it is primarily a response to loss of habitat area. The second prediction is based on marten foraging ecology. Although martens avoid large openings, they forage in regenerating clearcuts during summer (Soutiere 1979) and hunt along forest edges (Simon 1980, Spencer et al. 1983), and their diets are not restricted to forest-associated prey (Weckwerth and Hawley 1962, Koehler and Hornocker 1977, Buskirk and MacDonald 1984). Therefore, low levels of fragmentation may be beneficial to martens by increasing the abundance and diversity of small mammals. The third prediction assumes that martens respond to spatial pattern as well as loss of habitat, and that the combined effects would cause a greater reduction in martens from fragmented landscapes than that predicted from a response to loss of habitat alone.

Chapter 4 summarizes the effects of forest fragmentation on small mammals that serve as potential prey for the American marten. To date, investigations of the effects of

clearcutting on small mammals have focused on the scale of individual harvest blocks, comparing species richness or abundance between clearcut blocks and the original cover type (Gashwiler 1970, Petticrew and Sadleir 1974, Ramirez and Hornocker 1981, Gunther et. al 1983, Scrivner and Smith 1984, Walters 1991). Virtually nothing is known about small mammal responses to clearcutting at a larger spatial scale, in which the number and placement of cut areas defines the configuration of the landscape. The small size and limited foraging range of most small mammals relative to clearcut patch size suggest that a response to large-scale patterns is unlikely. However, there is evidence that southern red-backed voles (*Clethrionomys gapperi*) and California red-backed voles (*Clethrionomys californicus*) are less abundant at forest-clearcut edges (Walters 1991, Mills 1995), implying a possible sensitivity to landscape pattern. I investigated the effects of forest fragmentation on small mammals by examining differences in small mammal numbers within 12 of the 18 landscapes used in the marten study.

The focus of my dissertation is on fragmentation of forest habitats, but my results are relevant to the broader topic of habitat fragmentation, a process that is affecting countless species of plants and animals worldwide. The landscape metrics discussed can be applied to any habitat over a wide range of spatial scales, and the studies conducted on American martens and their prey offer a feasible approach for investigating fragmentation effects for a variety of species.

LITERATURE CITED

Addicott, J. F., J. M. Aho, M. F. Antolin, D. K. Padilla, J. S. Richardson, and D. A. Soluk. 1987. Ecological neighborhoods: scaling environmental patterns. Oikos **49**:340-346.

Buskirk, S. W., and S. O. MacDonald. 1984. Seasonal food habits of marten in south-central Alaska. Canadian Journal of Zoology **62**:944-950.

Clark, T. W., and T. M. Campbell. 1979. Population organization and regulatory mechanisms of pine martens in Grand Teton National Park, Wyoming. Pages 293-295 *in* R. M. Linn, editor. Conference on scientific research in national parks. Volume 1. National Park Service Transactions and Proceedings Series 5, Washington, D. C., USA.

Collinge, S. K., and R. T. T. Forman. 1995. Changes in insect community composition in response to experimentally-altered spatial configuration of a native grassland habitat. Supplement to the Bulletin of the Ecological Society of America **76**:116.

Diffendorfer, J. E., M. S. Gaines, and R. D. Holt. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). Ecology **76**:827-839.

Drew, G. S. 1995. Winter habitat selection by American marten (*Martes americana*) in Newfoundland: why old growth? Dissertation. Utah State University, Logan, Utah, USA.

Gardner, R. H. and O'Neill, R. V. 1991. Pattern, process, and predictability: the use of

neutral models for landscape analysis. Pages 289-307 *in* M. G. Turner and R. H. Gardner, editors. Quantitative methods in landscape ecology. Springer-Verlag, New York, USA.

Gashwiler, J. S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecology **51**:1018-1026.

Gibson, D. J., S. L. Collins, and R. E. Good. 1988. Ecosystem fragmentation of oak-pine forest in the New Jersey Pinelands. Forest Ecology and Management **25**:105-122.

Gunther, P. M., B. S. Horn, and G. D. Babb. 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Science **57**:32-44.

Hargis, C. D., and D. R. McCullough. 1984. Winter diet and habitat selection of marten in Yosemite National Park. Journal of Wildlife Management **48**:140-146.

Harris, L. D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago, Illinois, USA.

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs **62**:447-502.

Jennersten, O. 1988. Pollination in *Dianthus deltoides* (Carophyllaceae): effects of habitat fragmentation on visitation and seed set. Conservation Biology **2**:359-366.

Koehler, G. M., and M. G. Hornocker. 1977. Fire effects on marten habitat in the Selway-Bitterroot Wilderness. Journal of Wildlife Management **41**:500-505.

Krummel, J. R., R. H. Gardner, G. Sugihara, R. V. O'Neill, and P. R. Coleman. 1987.

Landscape patterns in a disturbed environment. Oikos **48**:321-324.

Li, H., and J. F. Reynolds. 1993. A new contagion index to quantify spatial patterns of landscapes. Landscape Ecology **8**:155-162.

Lovejoy, S. 1982. Area-perimeter relation for rain and cloud areas. Science **216**:185-187.

Mandelbrot, B. B. 1983. The fractal geometry of nature. Freeman and Company, San Francisco, California, USA.

Milne, B. T. 1991. Lessons from applying fractal models to landscape patterns. Pages 199-235 *in* M. G. Turner and R. H. Gardner, editors. Quantitative methods in landscape ecology. Springer-Verlag, New York, USA.

Mills, L. S.. 1995. Edge effects and isolation: red-backed voles on forest remnants. Conservation Biology **9**:395-403.

O'Neill, R. V., J. R. Krummel, R. H. Gardner, G. Sugihara, B. Jackson, D. L. DeAngelis, B. T. Milne, M. G. Turner, B. Zygmunt, S. W. Christensen, V. H. Dale, and R. L. Graham. 1988. Indices of landscape pattern. Landscape Ecology **1**:153-162.

Petticrew, B. G., and R. M. F. S. Sadleir. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. I. Populations dynamics. Canadian Journal of Zoology **52**:107-118.

Plotnick, R. E., R. H. Gardner, and R. V. O'Neill. 1993. Lacunarity indices as measures of landscape texture. Landscape Ecology **8**:201-211.

Ramirez, P. Jr., and M. Hornocker. 1981. Small mammal populations in different-aged clearcuts in northwestern Montana. Journal of Mammalogy **62**:400-403.

Ripple, W. J., G. A. Bradshaw, and T. A. Spies. 1991. Measuring forest landscape patterns in the Cascade Range of Oregon, USA. Biological Conservation **57**:73-88.

Rosenberg, K. V., and M. G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. Pages 263-272 *in* J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin, USA.

Rylands, A. B., and A. Keuroghlian. 1989. Primate populations in continuous forest and forest fragments in Central Amazonia. Acta Amazonia **18:**291-308.

Saunders, D. A. 1989. Changes in the avifauna of a region, district, and remnant as a result of fragmentation of native vegetation: the wheatbelt of western Australia: a case study. Biological Conservation **50**:99-136.

Scrivner, J. H., and H. D. Smith. 1984. Relative abundance of small mammals in four successional stages of spruce-fir forest in Idaho. Northwest Science **58**:171-176.

Shannon, C. E., and W. Weaver. 1962. The mathematical theory of communication. University of Illinois Press, Urbana, Illinois, USA.

Simon, T. L. 1980. An ecological study of the marten in the Tahoe National Forest, California. Thesis. California State University, Sacramento, California, USA.

Snyder, J. E., and J. A. Bissonette. 1987. Marten use of clear-cuttings and residual forest stands in western Newfoundland. Canadian Journal of Zoology **65**:169-174.

Soutiere, E. C. 1979. Effects of timber harvesting on marten in Maine. Journal of Wildlife Management **43**:850-860.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. Journal of Wildlife Management **47**:1181-1186.

Stauffer, D. 1985. Introduction to percolation theory. Taylor and Francis, London, United Kingdom.

Steventon, J. D., and J. T. Major. 1982. Marten use of habitat in a commercially clear-cut forest. Journal of Wildlife Management **46**:175-182.

Thompson, I. D., and P. W. Colgan. 1994. Marten activity in uncut and logged boreal forests in Ontario. Journal of Wildlife Management **58**:280-288.

Thompson, I. D., and A. S. Harestad. 1994. Effects of logging on American martens, and models for habitat management. Pages 355-367 *in* S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, New York, USA.

Verboom, B., and R. van Apeldoorn. 1990. Effects of habitat fragmentation on the red squirrel *Sciurus vulgaris*. Landscape Ecology **4**:171-176.

Voss, R. F. 1988. Fractals in nature: from characterization to simulation. Pages 21-70 *in* H. O. Peitgen, and D. Saupe, editors. The science of fractal images. Springer-Verlag, New York, USA.

Walters, B. B. 1991. Small mammals in a subalpine old-growth forest and clearcuts. Northwest Science **65**:27-30.

Weckwerth, R. P., and V. D. Hawley. 1962. Marten food habits and population fluctuations in Montana. Journal of Wildlife Management **26**:55-74.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D.

Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-205 *in* R. L. Burgess and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Ecological Studies 41. Springer-Verlag, New York, USA.

Wiens, J. A., N. C. Stenseth, B. van Horne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos **66**:369-380.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237-256 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates Incorporated, Sunderland, Massachusetts, USA.

CHAPTER 2

THE BEHAVIOR OF LANDSCAPE METRICS COMMONLY USED IN THE STUDY OF HABITAT FRAGMENTATION[1]

Abstract

Landscape metrics, developed for quantifying specific aspects of landscape pattern, have been applied to studies of habitat fragmentation without a clear understanding of what these measures provide. A meaningful interpretation is possible only when the limitations of each measure are fully understood, the range of attainable values is known, and the user is aware of potential shifts in the range of values due to characteristics of landscape patches. To examine the behavior of landscape metrics, I generated artificial landscapes that mimicked fragmentation processes while allowing me to control the size and shape of patches in the landscape and the mode of disturbance growth. I developed nine series of increasingly fragmented landscapes and used these to investigate the behavior of edge density, contagion, mean nearest neighbor distance, mean proximity index, perimeter-area fractal dimension, and mass fractal dimension. I found that most of the measures were highly correlated, especially contagion and edge density, which had a near-perfect inverse correspondence. Many of the measures were linearly associated with increasing disturbance until the proportion of disturbance on the landscape was approximately 0.40, with nonlinear associations at higher proportions due to percolation

---

[1]Coauthored by Christina D. Hargis, John A. Bissonette, and John L. David.

of the disturbance. None of the measures was able to differentiate between landscape patterns characterized by dispersed versus aggregated patches. The highest attainable value of each measure was altered by either patch size or shape, and in some cases, by both attributes. I summarize these findings by discussing the utility of each metric in providing information about habitat fragmentation.

1. Introduction

Investigations of ecological phenomena at the landscape scale often require quantifiable descriptions of landscape pattern and structure for testing relationships or making predictions about the landscape and the phenomena in question. To this end, several landscape metrics have been developed (Forman and Godron 1986; O'Neill *et al.* 1988; Turner 1990; Milne 1991; Gustafson and Parker 1992; Li and Reynolds 1993, McGarigal and Marks 1995).

Landscape metrics have been applied to investigations of habitat fragmentation, which was originally defined as the formation of isolated fragments from a formerly continuous habitat (Wilcox 1980). In that context, metrics were used to quantify the size, shape, and isolation of remnant patches of original habitat. I define habitat fragmentation and the use of landscape metrics more broadly, reflecting the growing interest in landscapes where the original habitat is not insular, but represents the landscape matrix (Franklin and Forman 1987; Ripple *et al.* 1991; Spies *et al.* 1994; Wallin *et al.* 1994).

In the fullest sense, fragmentation is the disruption of continuity (Lord and Norton 1990). When applied to the domain of landscapes, fragmentation is the disruption in

continuity of a land cover type by the presence of one or more disturbance types, and is manifest as a decline in the proportional representation of the original cover type on the landscape. Habitat fragmentation occurs along a continuum, beginning with matrix fragmentation, when the habitat of interest forms the landscape matrix, and disturbance takes the form of patches, and progresses into isolate fragmentation, in which the habitat of interest is reduced to remnant patches. Under this expanded definition, the focus is on holistic landscape pattern rather than patch characteristics.

The expected behavior of landscape metrics has been determined largely through mathematical proofs and from maps generated by the random placement of pixels (random pixel maps), the latter being a means of investigating each measure at fixed proportions of the disturbance cover type (Gardner and O'Neill 1991, Gustafson and Parker 1992). It generally has been assumed that the range of values associated with actual landscapes would be similar to those generated from random pixel maps. However, this assumption is questionable because ecological or anthropogenic processes that act to form real landscapes result in different interspersion patterns among patches than occur randomly.

To examine landscape metrics under more realistic conditions, I supervised the development of a computer program under the name Landscape Simulator for Fragmentation (LSF) that generated artificial landscapes under a variety of constraints that mimicked the formation of disturbance patches through both natural and anthropogenic processes. Using these maps, I investigated the behavior of landscape metrics that commonly are applied in studies of habitat fragmentation. The simulations allowed me to increase the proportional representation of a disturbance cover type while systematically

controlling patch size, shape, and placement so that I could isolate the effects of these parameters on the range of values associated with each landscape metric.

For each landscape metric examined, I asked the following questions:

1) Does the size or shape of landscape patches alter the possible range of values of the metric?
2) Does the mode of disturbance growth alter the possible range of values of the metric?
3) Does the metric provide unique information about fragmentation, as evidenced by low correlation with other landscape measures?
4) Is the metric sensitive to the spatial distribution of patches?

My goal in addressing these questions was to provide a greater understanding of the strengths and limitations of landscape metrics used for quantifying the process of habitat fragmentation.

2. Methods

2.1. Generating landscapes

The LSF program began with a map filled by a single cover type *i*, which formed the map matrix and represented the original cover type, and disturbed the continuity of this matrix with cover type *j*. It randomly selected patches of type *j* from a database and placed each patch at a random point on the map until a desired proportion of disturbance was reached. Each successive landscape represented an incremental increase in the proportion of disturbance (P_j) from 0.05-0.95 of the map, at 0.10 proportional intervals.

The actual P_j for each landscape was constrained to fall no more than 0.006 below the specified value.

Disturbance patches used for building fragmented landscapes conformed to one of three possible patch types, and each landscape was built from only one type. The first type consisted of small rectangles similar to the random clump maps developed by Gustafson and Parker (1992). The database consisted of 75 rectangular patches ranging in size from 1-25 pixels with edge lengths of 1-5 pixels (Fig. 2.1).

The second patch type was characterized by small, irregular-shapes with the same patch size frequency distribution as the database of rectangular patches (Fig. 2.2). The mean patch size of both rectangular and small-irregular patches was 9 ± 6.4 pixels.

The third patch type was created to simulate habitat fragmentation resulting from the clearcut method of timber harvest commonly used in managed forest ecosystems (Fig. 2.3). To generate realistic clearcut landscapes, I created a database of 109 actual timber clearcut harvest patches from the Uinta Mountains of northern Utah. Clearcut patch size ranged from 0.6-36 ha (7-400 pixels) with a mean of 10 ± 6.9 ha (115 ± 76.3 pixels), and the patch size frequency distribution was controlled to be the same as that derived from a subset of eighteen 9-km^2 landscape windows in the Uinta Mountains.

Clearcut patches from the Uinta Mountains were typical of harvest blocks located on National Forest System lands in western states. On federal lands, the current upper limit of clearcut harvest blocks for most forest types is 16 ha (40 acres), set by 36 CFR Part 219 (U.S. Department of Agriculture 1982) under the National Forest Management Act of 1976. Clearcuts greater than 16 ha occasionally are approved at the regional level

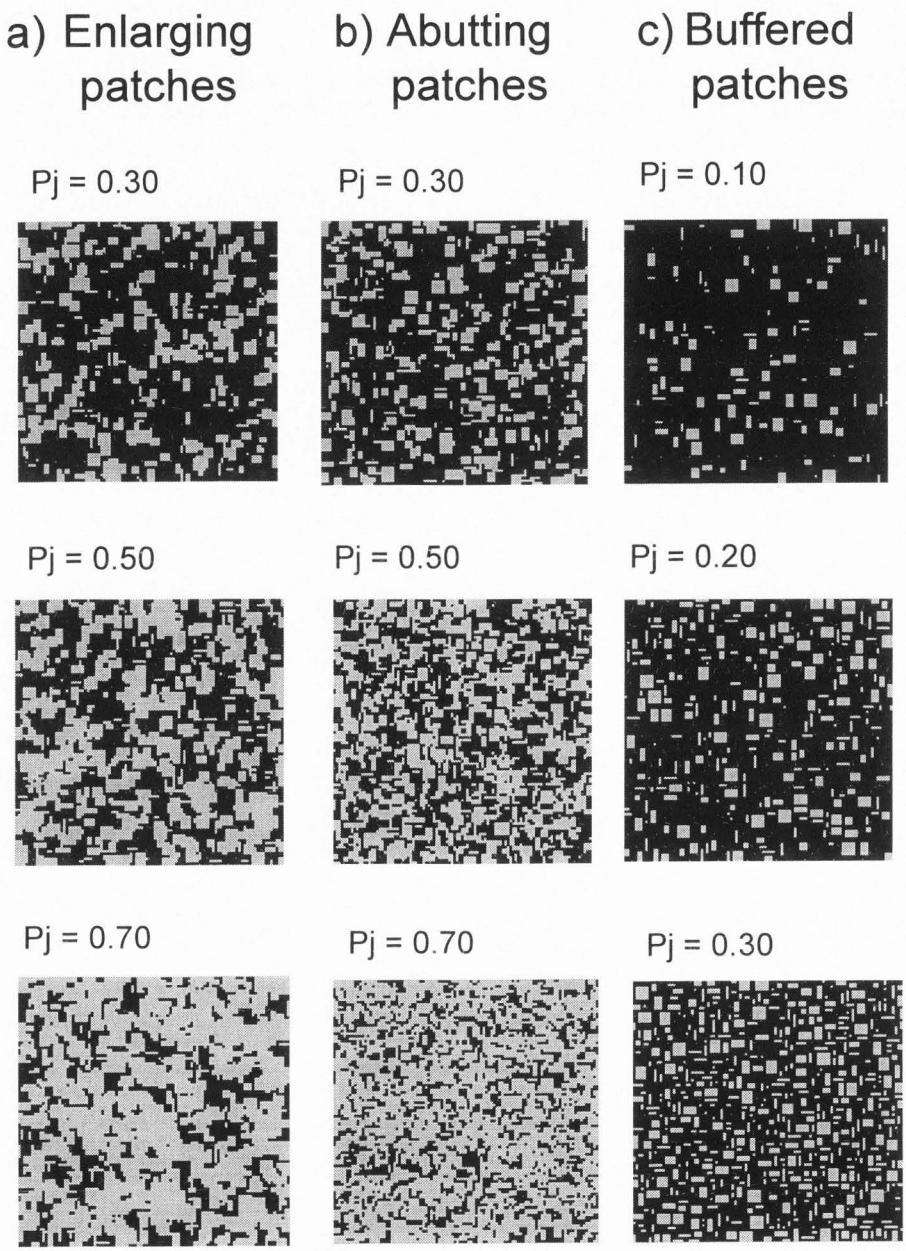


Fig. 2.1. Examples of landscape simulations using rectangular patches. Each row represents an increase in disturbance (P_j, shown in light gray) and each row illustrates a different mode of disturbance growth: a) enlarging patches; b) abutting patches; and c) buffered patches.

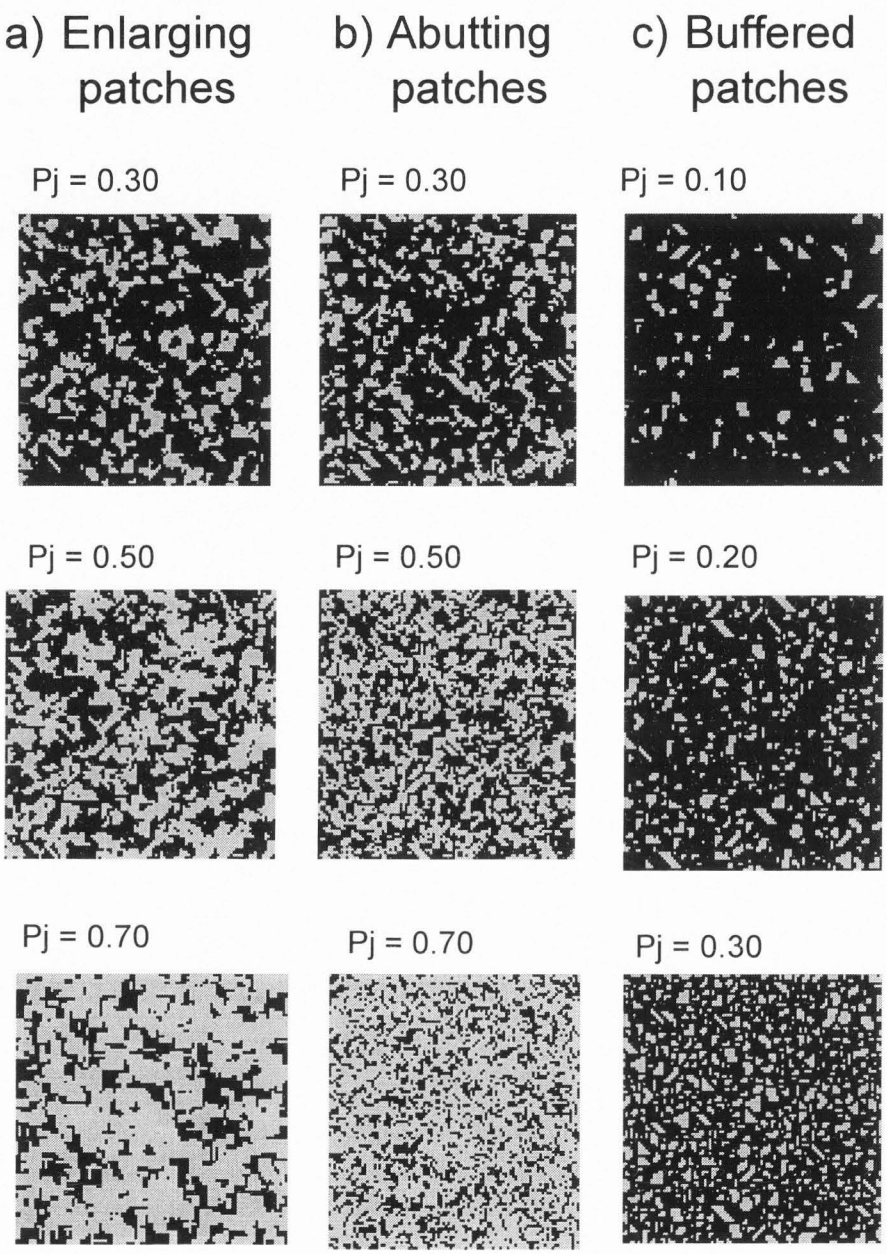


Fig. 2.2. Examples of landscape simulations using small, irregular-shaped patches. Each row represents an increase in disturbance (P_j, shown in light gray) and each row illustrates a different mode of disturbance growth: a) enlarging patches; b) abutting patches; and c) buffered patches.

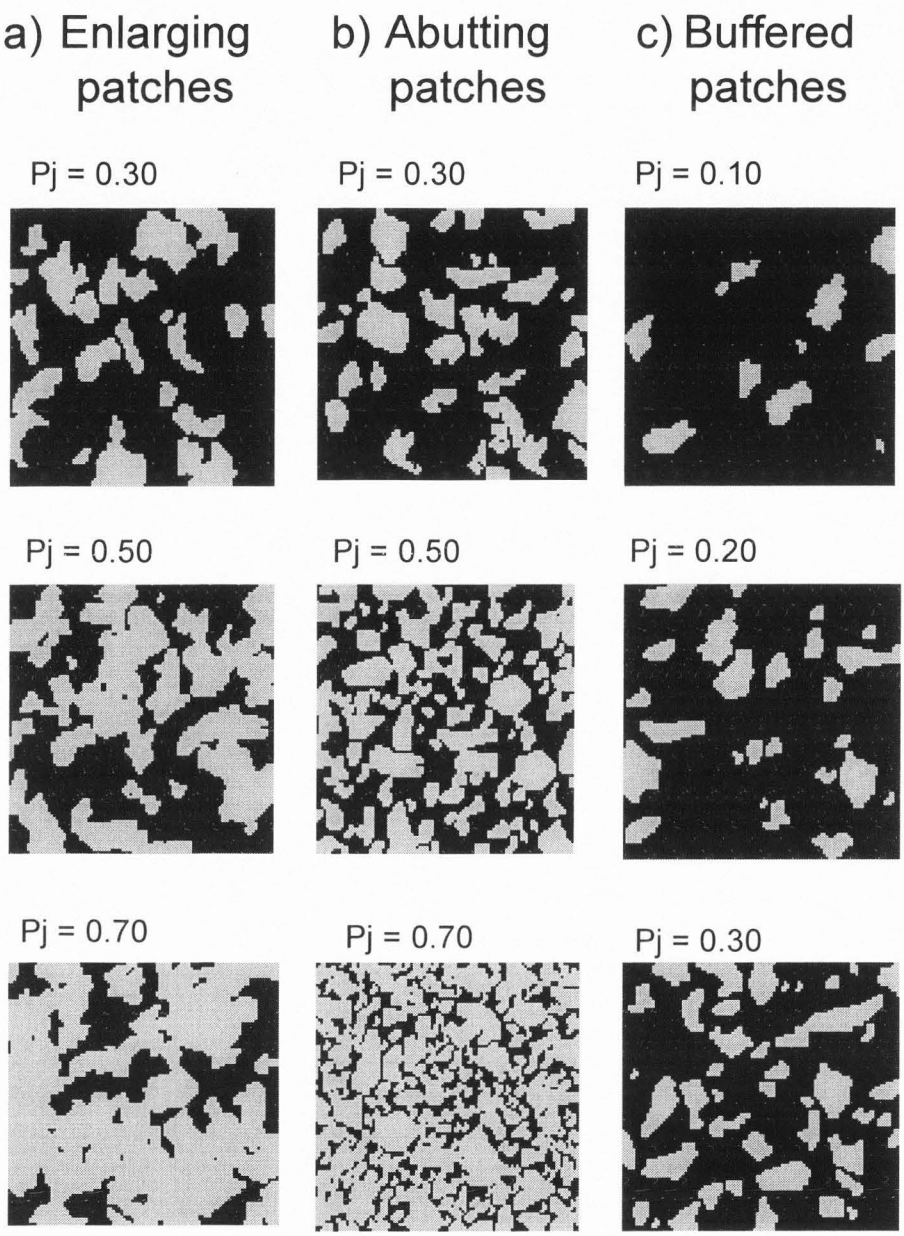


Fig. 2.3. Examples of landscape simulations using clearcut patches from the Uinta Mountains of northern Utah. Each row represents an increase in disturbance (P_j, shown in light gray) and each row illustrates a different mode of disturbance growth: a) enlarging patches; b) abutting patches; and c) buffered patches.

of the Forest Service with adequate justification. Economic considerations, as well as the difficulty in accurately mapping small tracts of land, typically create a lower size limit of 2 ha (5 ac), although exceptions below this size occur. The shapes of clearcut patches are often irregular, either from the standpoint of landscape design for scenic values, or due to topographic constraints. With all three databases, the patches were internally contiguous; that is, they did not contain internal areas occupied by cover type *i*.

In addition to modeling three types of patch configuration, I modeled three types of disturbance growth. On actual landscapes, disturbance can increase in a number of ways, including the enlargement of existing patches of disturbance, the addition of new patches immediately adjacent to previous disturbance patches, and the addition of new patches that are spatially isolated or buffered from previous disturbance patches. Landscapes with enlarging patches are typical of disturbances that spread from nuclei, such as fire and insect infestations. Landscapes with buffered patches are created from discrete disturbance events, such as the clearcut method of timber harvest, in which each cut block is a discrete unit separated from other cut blocks by forest buffers. Landscapes formed from abutting patches represent an intermediary stage between enlarging and buffered patch disturbance growth.

In my simulations, disturbance growth patterns were modeled by establishing rules in which patches were placed on a landscape. To simulate patch enlargement, I allowed patches to overlap as they were placed on the map (Figs. 2.1a, 2.2a, 2.3a). For abutting patches, the added patches could share boundaries with existing patches, but overlap was not allowed (Figs. 2.1b, 2.2b, 2.3b). To mimic buffered patches, each successive patch

was placed a minimum of two pixels from existing patches (Figs. 2.1c, 2.2c, 2.3c).

I built nine landscape series of increasing disturbance, using one patch type and disturbance growth pattern per series. Each series consisted of five landscape simulations at each proportional interval of disturbance. Due to constraints imposed by the abutting and buffered patch rules, not all landscapes reached disturbance levels of 0.95. For clearcut patch landscapes built with the abutting patch rule, the landscape series was truncated at a maximum patch density of 0.70 because clearcut patches were too large to fit in the remaining matrix unless patch overlap was allowed. The buffered patch rule constrained the maximum disturbance attainable for all landscapes, because irregular patch shapes left isolates of original habitat too small for additional patches. Moreover, buffers between patches occupied more than half of each landscape. P_j did not exceed 0.40 for landscapes built with clearcut patches, and was limited to 0.35 for rectangular patch maps and 0.30 for small-irregular patch maps. Because of the narrower range of P_j for landscapes made from buffered patches, I increased disturbance at increments of 0.05 rather than 0.10 while maintaining five landscapes per increment.

The buffered-patch rule altered the patch size distribution when the proportion of disturbance was high. As landscapes approached the maximum P_j, smaller patches were used to fill the remaining space, and the average patch size of the resulting landscapes was smaller than that of other landscapes.

Random placement of patches on landscapes generally resulted in dispersed patterns that were not useful for determining whether fragmentation measures could differentiate landscape pattern caused by aggregated versus dispersed patches. To test for sensitivity

to patch distribution, I created an additional landscape series of clearcut patches in which I forced patches to be aggregated. I used the buffered patch placement rule and specified that all patches be no further than three pixels apart (Fig. 2.4). I then compared the aggregated patterns with the original series of buffered, clearcut landscapes in which the patches were spatially dispersed.

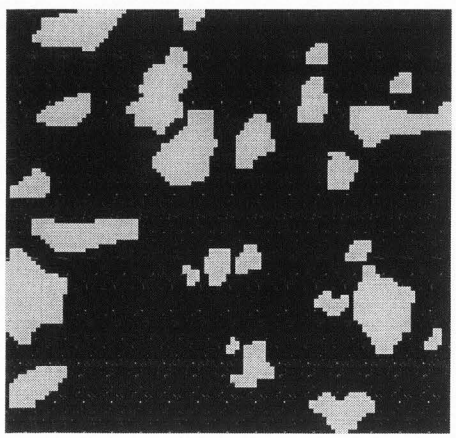
The LSF program was designed to imitate raster-based GIS maps of any user-defined size. My simulations were 101 by 101 pixels in extent with 30-m resolution to approximate a map extent and grain size of interest to ecologists using thematic mapper data on study areas the size of individual watersheds, timber sales, and fire events. These 101^2-pixel maps were used for the majority of my investigations of fragmentation metrics, but I also created series of landscapes on maps of 64^2, 128^2, 256^2, and 512^2 pixels to test the effects of map extent on the behavior of the measures.

LSF was written by J. David in the Khoros® image processing environment on Sun Sparc stations. Simulations were run on an IBM RS6000/370 network at the Albuquerque Resource Center, University of New Mexico.

2.2. Measuring fragmentation

Landscape measures selected for analysis were edge density, contagion, mean nearest neighbor distance, proximity index, perimeter-area fractal dimension, and mass fractal dimension, which are defined below. I used the FRAGSTATS spatial pattern analysis program ver. 2.0 (McGarigal and Marks 1995) to calculate the first five measures listed. Algorithms used in these calculations are listed in Appendix C of the FRAGSTATS

a)



b)

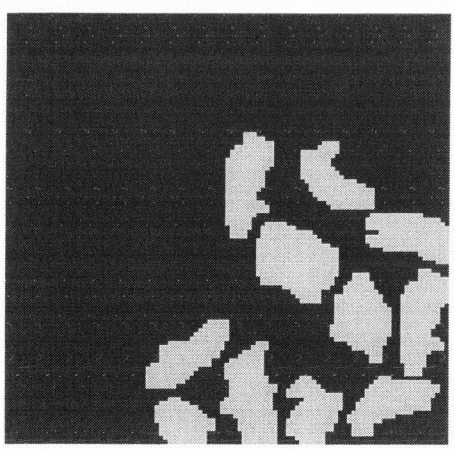


Fig. 2.4. Landscapes with $P_j = 0.20$ where patches are a) dispersed and b) aggregated.

manual (McGarigal and Marks 1995). I calculated mass fractal dimension using software developed by B. Milne and T. Keitt, University of New Mexico, under NSF grant BSR-9107339, which they included as an add-on toolbox within the Khoros image processing environment.

Edge density is the total length of patch edge per unit area within each landscape (McGarigal and Marks 1995), which I expressed as km/ha. This measure is sensitive to map resolution, since fine resolution yields greater edge length, and is therefore useful only for comparison between landscapes with a common grain size. I calculated edge density using pixels connected both side to side and diagonally.

Contagion is an index designed to quantify the degree of aggregation found within landscape classes, originally formulated by O'Neill *et al.* (1988) and later modified by Li and Reynolds (1993). Requiring raster-format landscapes for calculation, it is the probability that two, randomly chosen adjacent pixels belong to the same class. In FRAGSTATS, calculations involve the product of two probabilities: 1) the probability that a randomly selected pixel belongs to a given class, which is equivalent to the proportional representation of each class, and 2) the conditional probability that, given a pixel is of one class, that an adjacent pixel is of a differing class (McGarigal and Marks 1995). Contagion index values range between 0-100% of the maximum aggregation possible, with maximum aggregation occurring when a landscape is entirely occupied by a single class or cover type (Ritters *et al.* 1996).

Mean nearest neighbor distance defines the average edge-to-edge distance (m) between a patch and its nearest neighbor in the landscape. It differs from the mean

proximity index in that patch area is not used in the calculation, and distances are between nearest patches rather than between all patches within a search radius. This index yields absolute values and requires maps of the same resolution if landscapes are compared.

The proximity index (Whitcomb *et al.* 1981; Gustafson and Parker 1992) measures the isolation of a patch within a complex of patches, given a specified search radius. It is calculated as the sum, for all patches within the search radius, of the area of each patch divided by the square of the nearest edge-to-edge distance between it and the patch being indexed. The mean proximity index for a landscape is the average proximity index derived from all patches. Comparisons between maps are possible if maps are at the same resolution and the search radius is the same. I used a search radius of 10 pixels to allow comparison of my results with those of Gustafson and Parker (1992). However, FRAGSTATS (McGarigal and Marks (1995) calculated the distances from a focal patch to each patch within the search radius, whereas Gustafson and Parker (1992) calculated the nearest neighbor distance of all patches within the search radius. Using FRAGSTATS, I was unable to standardize the proximity index in the manner described by Gustafson and Parker (1992), and instead conducted the analysis on the absolute values of the proximity index. Patch areas were calculated using connections of pixels on the four adjacent sides and diagonals.

Perimeter-area fractal dimension provides information on the irregularity of patch edge. Perimeter-area fractal dimension was computed by FRAGSTATS as 2 divided by the slope of log(P) on log(A), where P and A are the perimeter (m) and area (m^2) of each patch (McGarigal and Marks 1995). The theoretical limits of this measure are between

one and two, with higher values indicating greater complexity of patch edge (Lovejoy 1982). The term "perimeter" in McGarigal and Marks (1995) is used to describe the outermost occupied pixels of a patch, whereas in the physics literature, these pixels are known as a special form of edge called the "hull," and the term "perimeter" is reserved for the unoccupied pixels adjacent to the hull (Voss 1984; Grossman and Aharony 1987). I will retain the term perimeter-area fractal dimension in reference to the measure calculated by FRAGSTATS, but will refer to the outermost occupied pixels of a patch as the edge rather than the perimeter.

Mass fractal dimension quantifies total complexity of the map matrix rather than irregularity of individual patches. This measure describes the scaling relationship between the number of pixels of a given cover type within a sample of the landscape, and the size of the box defining the sample. Box sizes range from a minimum of 3-5 pixels on a side, to a maximum of approximately 1/3 of the landscape. I calculated mass fractal dimension for cover type *i* using sampling boxes with edge lengths of 3, 9, 15, 21, and 27 pixels. I counted all pixels of cover type *i* within the box when it was centered on each *i* pixel on the map, and derived a mean value of total *i* pixels per box size. Mass fractal dimension was the slope derived from regressing the log of the mean number of pixels in each size of box on the log of the box lengths (Voss 1988; Milne 1991).

The theoretical limits of this measure lie between zero and two. A value of two is achieved when the cover type of interest completely fills the two-dimensional map or occurs in a regular pattern that covers the entire map, and lower values are derived when either of these conditions is altered by the presence of a second cover type.

2.3. Analyzing the behavior of fragmentation measures

I analyzed the behavior of each fragmentation measure over the full range of disturbance by regressing each measure against increasing P_j within each landscape series. I examined the effects of patch size and patch shape by using multiple regression techniques to compare fragmentation values generated by rectangular, small-irregular, and clearcut patch configurations. Where significant differences in the values of a fragmentation measure occurred among patch configurations, I conducted pairwise comparisons of regression coefficients using a Fisher's LSD (Kleinbaum *et al.* 1988) to determine the source of the difference.

I added a quadratic term to the regression models for the analysis of contagion, total edge, mass fractal dimension, and perimeter-area fractal dimension to make a better fit of the data to the regression line. For nearest neighbor distance, a log-log transformation was applied to account for nonlinearity in the response curves. I was unable to conduct a regression analysis on mean proximity index because of the high variance in observed values at high values of P_j, and chose to analyze this variable qualitatively.

I compared the effects of each type of disturbance growth qualitatively rather than through a regression analysis, because landscape series using abutting and discrete patches did not cover the full range of P_j. This was done through a visual comparison of the fragmentation measures' response curves generated for landscapes under each of the patch placement rules.

3. Results

3.1. Effects of patch size

The size of patches involved in the fragmentation process significantly altered the range of values of each fragmentation measure when applied to each series of landscapes ($P < 0.001$) (Tables 2.1, 2.2, and 2.3). This was determined by statistically comparing values obtained from landscapes built from clearcut patches with those obtained from the small-patch landscapes of either rectangles or small-irregular patches.

The larger size of clearcut patches yielded consistently lower values of edge density and higher values of contagion over the full range of landscape fragmentation than either of the smaller patch landscapes (Fig. 2.5). Mean nearest neighbor distance appeared to be sensitive to patch size only when patches were sparsely distributed (low P_j) (Fig. 2.5), resulting in more variation in inter-patch distance for large-patch landscapes. Landscapes containing few, large clearcuts had higher mean distances between patches than landscapes containing many, small clearcuts.

The proximity index also was sensitive to patch size, with large-patch landscapes having higher values and greater variance than small-patch landscapes at all levels of disturbance and under all modes of disturbance growth (Fig. 2.6). Perimeter-area fractal dimension values were lower for large-patch landscapes when disturbance patches enlarged or were abutting. This relationship was reversed when patches were buffered, and large-patch landscapes had increasingly higher fractal dimension values than small-patch landscapes as disturbance increased (Fig. 2.6).

Mass fractal dimension was fairly insensitive to differences in patch size, yielding

Table 2.1. Comparison of fragmentation measures when the overlapping patch placement rule is used to construct landscapes. Comparisons are between rectangular-patch landscapes (R), small-irregular-patch landscapes (S), and clearcut-patch landscapes (C).

Variables	Model[a]	R^2	d.f.	F	p > F	T-test	Comparison	T	p > T
Edge density	$Y = T + P + P^2 + TP + TP^2$	0.99	8, 141	1701.9	0.001	R vs S	Patch shape	-6.35	0.001
						S vs C	Patch size	-29.93	0.001
						R vs C	Size and shape	-23.59	0.001
Contagion	$Y = T + P + P^2 + TP + TP^2$	0.99	8, 141	4012.2	0.001	R vs S	Patch shape	2.56	0.012
						S vs C	Patch size	16.38	0.001
						R vs C	Size and shape	13.82	0.001
Near neigh. dist.	$\ln(Y) = T + \ln(P) + T \ln(P)$	0.92[b]	5, 144	342.3	0.001	R vs S	Patch shape	-0.23	0.814
						S vs C	Patch size	10.91	0.001
						R vs C	Size and shape	10.07	0.001
Perim-area fractal	$Y = T + P + P^2 + TP$	0.93	6, 143	302.3	0.001	R vs S	Patch shape	-5.53	0.001
						S vs C	Patch size	24.07	0.001
						R vs C	Size and shape	5.79	0.001
Mass fractal	$Y = T + P + P^2 + TP$	0.98	6, 128	879.4	0.001	R vs S	Patch shape	1.01	0.317
						S vs C	Patch size	4.75	0.001
						R vs C	Size and shape	4.17	0.001

[a] Y = the fragmentation measure, T = patch type (n = 50 for each type) and P = the proportion of the map disturbed by patch placement.
[b] Derived from log scale.

Table 2.2. Comparison of fragmentation measures when the abutting patch placement rule is used to construct landscapes. Comparisons are between rectangular-patch landscapes (R, n = 50), small, irregular-patch landscapes (S, n = 50), and clearcut-patch landscapes (C, n = 40).

Variables	Model[a]	R^2	d.f.	F	p > F	T-test	Comparison	T	p > T
Edge density	$Y = T + P + P^2 + TP + TP^2$	0.96	8, 161	544.4	0.001	R vs S	Patch shape	-4.05	0.001
						S vs C	Patch size	-18.52	0.001
						R vs C	Size and shape	-15.64	0.001
Contagion	$Y = T + P + P^2 + TP + TP^2$	0.99	8, 161	4996.5	0.001	R vs S	Patch shape	2.94	0.004
						S vs C	Patch size	22.35	0.001
						R vs C	Size and shape	20.27	0.001
Near neigh. dist.	$\ln(Y) = T + \ln(P) + T \ln(P)$	0.95[b]	5, 164	596.2	0.001	R vs S	Patch shape	-0.62	0.539
						S vs C	Patch size	13.59	0.001
						R vs C	Size and shape	12.74	0.001
Perim-area fractal	$Y = T + P + P^2 + TP + TP^2$	0.93	8, 161	282.5	0.001	R vs S	Patch shape	-4.91	0.001
						S vs C	Patch size	-4.68	0.001
						R vs C	Size and shape	-5.57	0.001
Mass fractal	$Y = T + P + TP$	0.98	5, 154	1725.3	0.001	R vs S	Patch shape	6.79	0.001
						S vs C	Patch size	15.70	0.001
						R vs C	Size and shape	9.01	0.001

[a] Y = the fragmentation variable, T = patch type, and P = the proportion of the landscape disturbed by patch placement.
[b] Derived from log scale.

Table 2.3. Comparison of fragmentation measures when the buffered patch placement rule is used to construct landscapes. Comparisons are between rectangular-patch landscapes (R, n = 35), small-irregular-patch landscapes (S, n = 35), and clearcut-patch landscapes (C, n = 40).

Variables	Model[a]	R^2	d.f.	F	p > F	T-test	Comparison	T	p > T
Edge density	$Y = T + P + P^2 + TP + TP^2$	0.99	8, 96	4139.8	0.001	R vs S	Patch shape	-7.16	0.001
						S vs C	Patch size	3.94	0.001
						R vs C	Size and shape	6.87	0.001
Contagion	$Y = T + P_i + P^2 + TP + TP^2$	0.99	8, 96	12026.4	0.001	R vs S	Patch shape	2.91	0.005
						S vs C	Patch size	7.42	0.001
						R vs C	Size and shape	5.78	0.001
Near neigh. dist.	$\ln(Y) = T + \ln(P) + T \ln(P)$	0.95[b]	5, 99	389.7	0.001	R vs S	Patch shape	-1.25	0.215
						S vs C	Patch size	6.69	0.001
						R vs C	Size and shape	8.36	0.001
Perim-area fractal	$Y = T + P + P^2 + TP + TP^2$	0.87	8, 96	81.6	0.001	R vs S	Patch shape	13.03	0.001
						S vs C	Patch size	-9.13	0.001
						R vs C	Size and shape	3.98	0.001
Mass fractal	$Y = T + P_i + TP$	0.96	3, 61	461.3	0.001	R vs S	Patch shape	13.34	*
						S vs C	Patch size	*	*
						R vs C	Size and shape	*	*

[a] Y = the fragmentation variable, T = patch type, and P = the proportion of the landscape disturbed by patch placement.
[b] Derived from log scale.
* Qualitatively different; no statistical test performed; see text

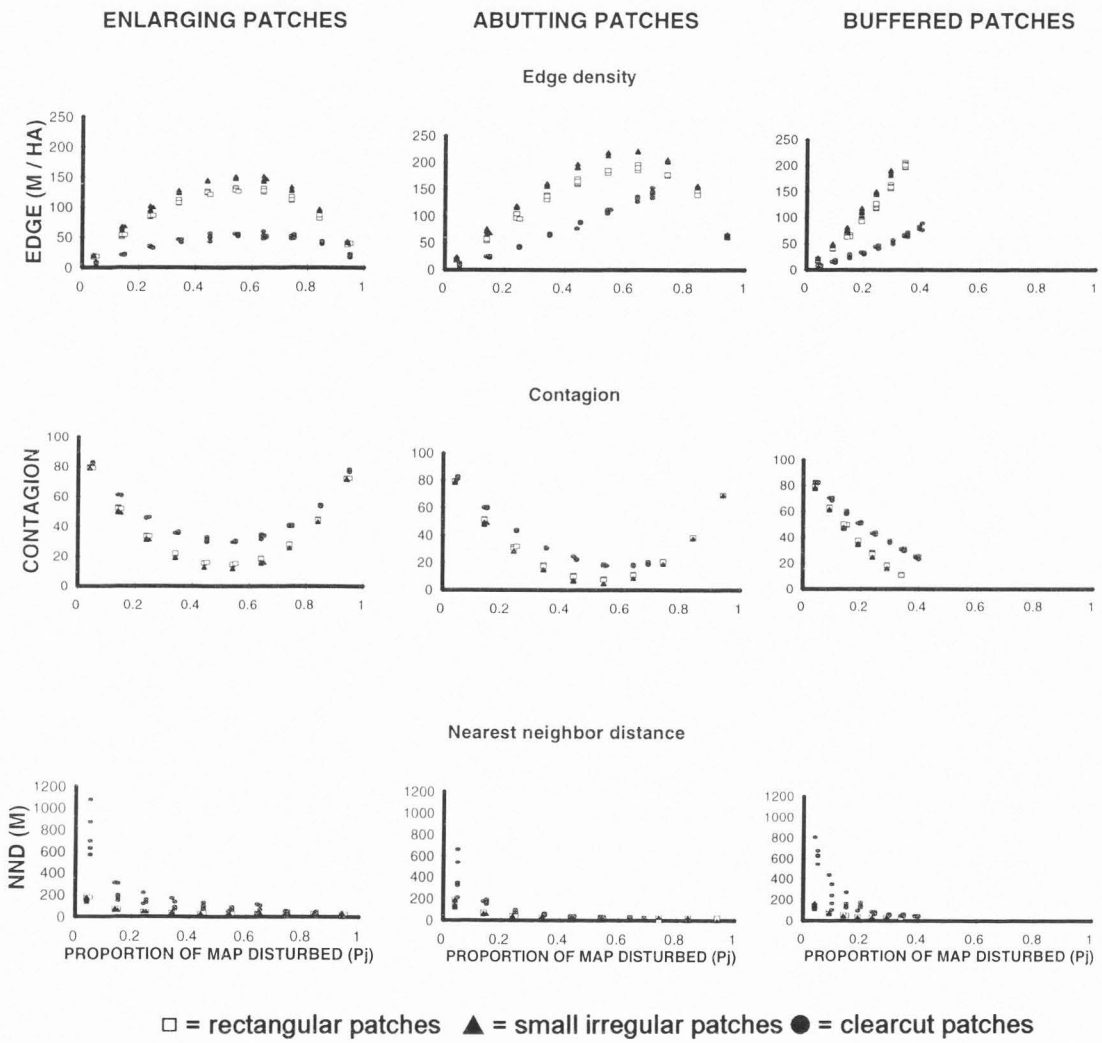


Fig. 2.5. Response curves for edge density, contagion, and mean nearest neighbor distance caused by differences in patch type (three patch types per graph) and mode of disturbance growth (three columns of graphs). See Fig. 2.7a for enlarged graph of mean nearest neighbor distance for rectangular and small, irregular-patch landscapes.

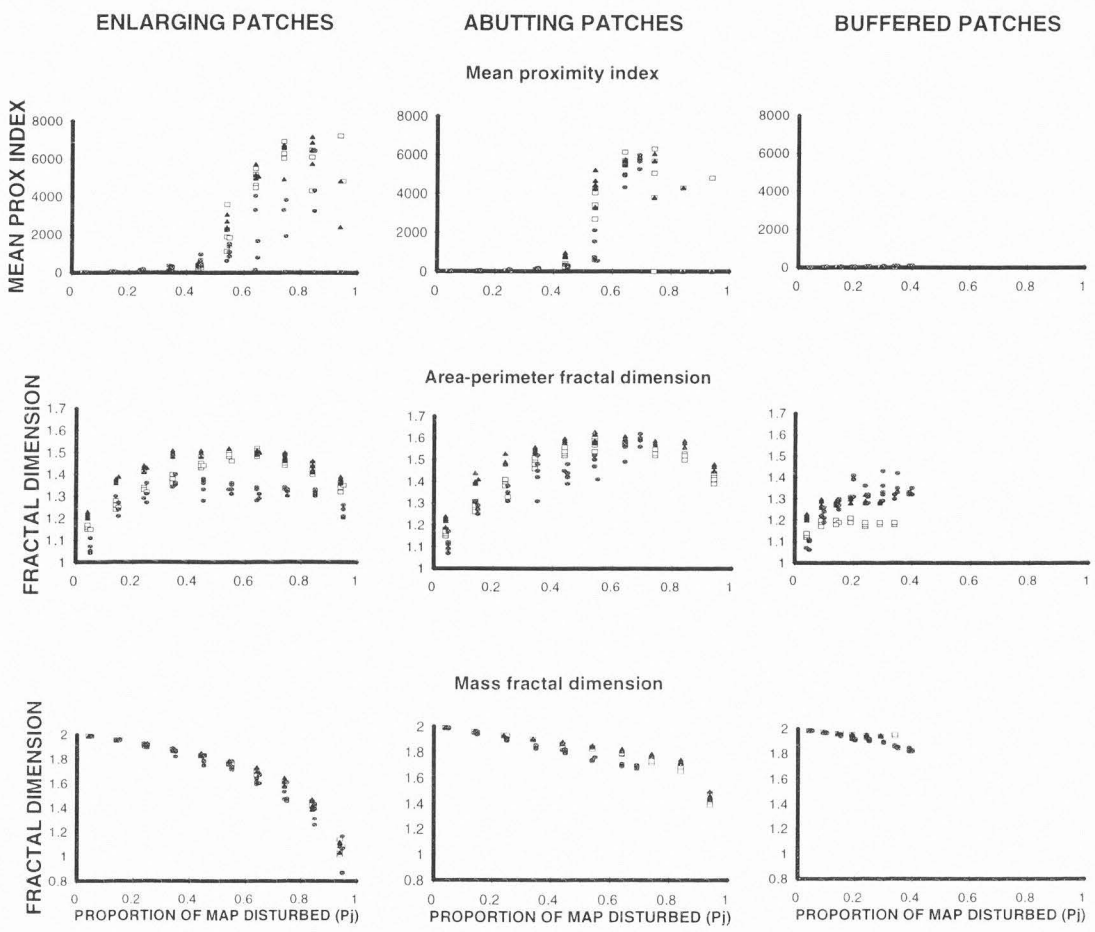


Fig. 2.6. Response curves for mean proximity index, perimeter-area fractal dimension, and mass fractal dimension caused by differences in patch type (three patch types per graph) and mode of disturbance growth (three columns of graphs). See Fig. 2.7b for enlarged graph of mean proximity index on buffered-patch landscapes.

similar-appearing response curves for both small-patch and large-patch landscapes (Fig. 2.6). Although I found a significant difference in slope for mass fractal dimension over increasing disturbance between clearcut landscapes and the two, small-patch landscapes, the significance was due to low variance in fractal values among landscapes, and the actual difference in fractal values was extremely small.

3.2. Effects of patch shape

I used rectangular patch and small-irregular patch landscapes to evaluate the effects of patch shape on fragmentation measures, since these patch types differed only in shape. I found significant differences in response curves for edge density, contagion, and perimeter-area fractal dimension under all modes of disturbance growth ($P < 0.001$) (Tables 2.1, 2.2, and 2.3). I found significant differences for mass fractal dimension only when disturbance increased through enlarging patches (Table 2.1).

I found no evidence that patch shape influenced the nearest neighbor distance measure or mean proximity index. Neither the slopes nor intercepts of rectangular or irregular patches were statistically different for the nearest neighbor distance measure (Tables 2.1, 2.2, and 2.3), and the response curves appeared similar (Fig. 2.7a).

3.3. Effects from type of disturbance growth

I identified differences due to type of disturbance growth for most of the fragmentation measures tested, either in the magnitude of the observed values or in the general shapes of the response curves. Landscapes with enlarging patches had less edge density than those with abutting or buffered patches (Fig. 2.5). Type of disturbance

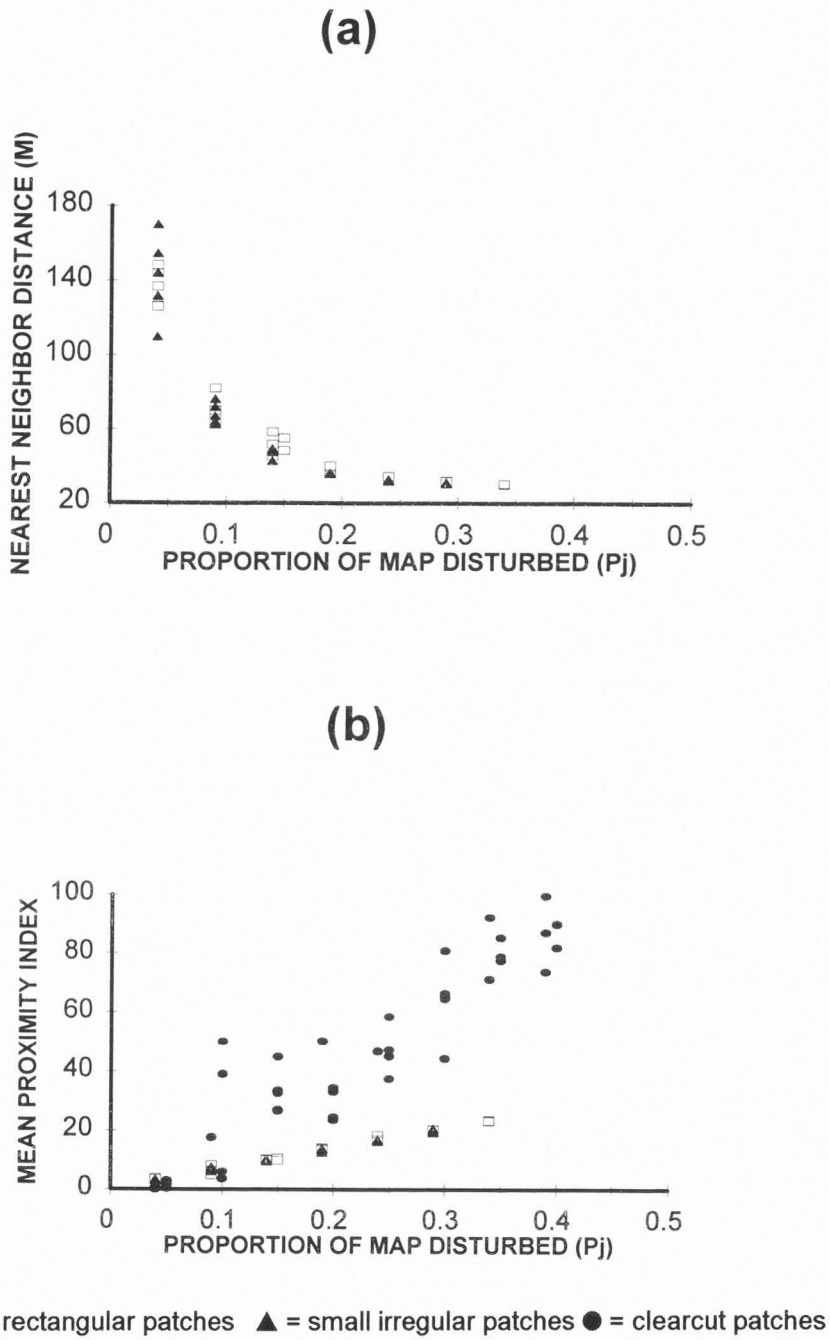


Fig. 2.7. Enlarged scale for a) mean nearest neighbor distance and b) mean proximity index when disturbance growth is with buffered patches.

growth also influenced the point of maximum edge density, occurring near $P_j = 0.60$ for enlarging patches, around $P_j = 0.65$ for abutting patch landscapes, and at the maximum P_j for buffered patch landscapes, between 0.30-0.40.

For contagion, type of disturbance growth had the most pronounced effect at mid-ranges of disturbance. For example, at $P_j = 0.35$, contagion of rectangular-patch landscapes was approximately 12% higher with enlarging patches than with buffered patches (Fig. 2.5).

For perimeter-area fractal dimension, type of disturbance growth affected both the magnitude of values and shape of response curves, especially for landscapes consisting of rectangular patches (Fig. 2.6). Enlarging and abutting patch rules allowed rectangles to coalesce into irregular shapes, resulting in higher perimeter-area fractal values than under the buffered patch rule, where original, rectangular shapes were maintained. The abutting patch rule yielded higher fractal dimension values than either the overlapping or buffered patch rules. Response curves were flattest for buffered patch landscapes.

Mass fractal dimension was minimally affected by type of disturbance growth. Enlarging patches yielded the greatest range of observed values, and was the only growth pattern that resulted in fractal dimension values < 1 (Fig. 2.6). This appeared to be an artifact of the small extent of 101 x 101 pixel maps. Using maps with either 256^2 or 512^2 pixels, the lowest values derived were 1.12 and 1.19, respectively, similar to those derived under the other growth models.

Mean nearest neighbor distance and mean proximity index appeared insensitive to type of disturbance growth. All landscape series yielded similar response curves and

similar ranges of values (Figs. 2.5, 2.6, and 2.7).

3.4. Correlations between fragmentation measures

Within each of the nine landscape series, I examined correlations between increasing proportions of disturbance and each landscape metric, as well as correlations between the metrics themselves (Tables 2.4, 2.5, and 2.6). All measures generally exhibited nonlinear relationships with increasing disturbance when patches enlarged (Figs. 2.5 and 2.6). The notable exception was mass fractal dimension, which exhibited a nearly linear relationship and high, negative correlation with enlarging patches (Tables 2.4, 2.5, and 2.6; Fig. 2.6).

When patches were buffered, all measures except mean nearest neighbor distance and perimeter-area fractal dimension were highly correlated with the amount of disturbance (Tables 2.4, 2.5, and 2.6; Figs. 2.5, 2.6, and 2.7b). Mean nearest neighbor distance exhibited exponential decay and the perimeter-area fractal dimension exhibited little change in values with increasing disturbance.

Among the six landscape metrics, correlations generally were lowest when patches enlarged, and were highest when patches were buffered. In particular, edge density, contagion, mean proximity index, and mass fractal dimension were highly correlated with one another on buffered-patch landscapes, because these measures all produced near-linear slopes at disturbance levels below the critical probability of percolation (Tables 2.4, 2.5, and 2.6; Figs. 2.5, 2.6, and 2.7b). When disturbance growth was with abutting patches, perimeter-area fractal dimension and mass fractal dimension were highly

Table 2.4. Correlation matrices of landscape metrics applied to rectangular-patch landscapes under three types of disturbance growth, with all r > 0.80 highlighted.

Enlarging patches

	P_j	Edge dens.	Contag.	Near. neigh. dist.	Prox. index	A-P fractal dim.	Mass fractal dim.
P_j	1.00	0.28	-0.13	-0.74	0.71	0.64	-0.91
Edge dens.		1.00	-0.98	-0.61	0.32	0.90	0.10
Contag.			1.00	0.55	-0.17	-0.82	-0.25
Near. neigh. dist.				1.00	-0.36	-0.79	0.58
Prox. index					1.00	0.54	-0.51
A-p fractal dim.						1.00	-0.30
Mass fractal dim.							1.00

Abutting patches

	P_j	Edge dens.	Contag.	Near. neigh. dist.	Prox. index	A-p fractal dim.	Mass fractal dim.
P_j	1.00	0.47	-0.19	-0.77	0.42	0.65	-0.92
Edge dens.		1.00	-0.93	-0.62	0.61	0.95	-0.13
Contag.			1.00	0.53	-0.45	-0.85	-0.14
Near. neigh. dist.				1.00	-0.21	-0.78	0.64
Prox. index					1.00	0.55	-0.22
A-p fractal dim.						1.00	-0.37
Mass fractal dim.							1.00

Buffered patches

	P_j	Edge dens.	Contag.	Near. neigh. dist.	Prox. index	A-p fractal dim.	Mass fractal dim.
P_j	1.00	0.99	-0.99	-0.83	0.99	0.53	-0.88
Edge dens.		1.00	-0.97	-0.78	0.99	0.49	-0.83
Contag.			1.00	0.89	-0.99	-0.61	0.93
Near. neigh. dist.				1.00	-0.84	-0.82	0.91
Prox. index					1.00	0.52	-0.89
A-p fractal dim.						1.00	-0.66
Mass fractal dim.							1.00

Table 2.5. Correlation matrices of landscape metrics on landscapes with irregular-shaped patches and three types of disturbance growth, with all r > 0.80 highlighted.

Enlarging patches

	P_j	Edge dens.	Contag.	Near. neigh. dist.	Prox. index	A-P fractal dim.	Mass fractal dim.
P_j	1.00	0.25	-0.12	-0.71	0.75	0.42	-0.91
Edge dens.		1.00	-0.99	-0.61	0.31	0.94	0.14
Contag.			1.00	0.57	-0.18	-0.92	-0.26
Near. neigh. dist.				1.00	-0.40	-0.81	0.53
Prox. index					1.00	0.33	-0.55
A-p fractal dim.						1.00	-0.08
Mass fractal dim.							1.00

Abutting patches

	P_j	Edge dens.	Contag.	Near. neigh. dist.	Prox. index	A-p fractal dim.	Mass fractal dim.
P_j	1.00	0.42	-0.16	-0.76	0.43	0.61	-0.89
Edge dens.		1.00	-0.94	-0.55	0.73	0.91	-0.03
Contag.			1.00	0.48	-0.55	-0.85	-0.19
Near. neigh. dist.				1.00	-0.23	-0.82	0.64
Prox. index					1.00	0.55	-0.11
A-p fractal dim.						1.00	-0.30
Mass fractal dim.							1.00

Buffered patches

	P_j	Edge dens.	Contag.	Near. neigh. dist.	Prox. index	A-p fractal dim.	Mass fractal dim.
P_j	1.00	0.99	-0.99	-0.82	0.99	0.68	-0.95
Edge dens.		1.00	-0.98	-0.79	0.99	0.65	-0.93
Contag.			1.00	0.88	-0.99	-0.75	0.97
Near. neigh. dist.				1.00	-0.85	-0.86	0.90
Prox. index					1.00	0.72	-0.95
A-p fractal dim.						1.00	-0.78
Mass fractal dim.							1.00

Table 2.6. Correlation matrices for landscape metrics applied to landscapes with clearcut patches, under three types of disturbance growth, with all r > 0.80 highlighted.

Enlarging patches

	P_j	Edge dens.	Contag.	Near. neigh. dist.	Prox. index	A-P fractal dim.	Mass fractal dim.
P_j	1.00	0.40	-0.12	-0.71	0.41	0.35	-0.91
Edge dens.		1.00	-0.94	-0.64	0.42	0.85	-0.04
Contag.			1.00	0.54	-0.27	-0.85	-0.23
Near. neigh. dist.				1.00	-0.27	-0.79	0.53
Prox. index					1.00	0.29	-0.25
A-p fractal dim.						1.00	-0.07
Mass fractal dim.							1.00

Abutting patches

	P_j	Edge dens.	Contag.	Near. neigh. dist.	Prox. index	A-p fractal dim.	Mass fractal dim.
P_j	1.00	0.99	-0.93	-0.74	0.75	0.92	-0.99
Edge dens.		1.00	-0.91	-0.70	0.77	0.91	-0.99
Contag.			1.00	0.87	-0.50	-0.92	0.92
Near. neigh. dist.				1.00	-0.35	-0.80	0.73
Prox. index					1.00	0.67	-0.75
A-p fractal dim.						1.00	-0.92
Mass fractal dim.							1.00

Buffered patches

	P_j	Edge dens.	Contag.	Near. neigh. dist.	Prox. index	A-p fractal dim.	Mass fractal dim.
P_j	1.00	0.99	-0.99	-0.77	0.93	0.73	-0.98
Edge dens.		1.00	-0.97	-0.73	0.93	0.67	-0.98
Contag.			1.00	0.84	-0.92	-0.80	0.96
Near. neigh. dist.				1.00	-0.78	-0.85	0.72
Prox. index					1.00	0.68	-0.91
A-p fractal dim.						1.00	-0.70
Mass fractal dim.							1.00

correlated with both contagion and edge density, ($r > 0.90$).

The inverse correlation between edge density and contagion is particularly noteworthy, because the graphed values of these measures are nearly mirror images of each other (Fig. 2.5). In landscapes using buffered, rectangular patches, these measures were nearly perfectly correlated ($r = -0.99$).

3.5. Sensitivity to the spatial distribution of patches

None of the measures provided useful information about the spatial distribution of patches, as evident in a comparison between landscapes with dispersed or aggregated patches (Fig. 2.8). Landscapes with aggregated patches had slightly lower edge density values than landscapes with dispersed patches, but the slopes of the response curves were nearly the same. Contagion values were also similar for both aggregated and dispersed patches. The slight differences between response curves for both of these measures were due to patch size rather than spatial pattern. Dispersed-patch landscapes used smaller patches to fill the remaining space when disturbance was high, resulting in slightly higher edge density and slightly lower contagion values.

Although mean nearest neighbor distance and mean proximity index both provided information on distances between patches, neither measure was able to distinguish the aggregated versus dispersed patterns because neither measure was designed to include landscape extent in the calculations of patch proximity. Thus, landscapes with low disturbance and tightly aggregated patches produced the same values as landscapes with high disturbance and dispersed patches, because at high disturbance, the distance between

patches was the same as that found on landscapes with few, clumped patches. For both measures, the aggregated patch pattern produced values across the full range of fragmentation that would have been expected only on high-disturbance landscapes (Fig. 2.8).

Neither of the measures of fractal dimension provided unique values for landscapes with aggregated versus dispersed patches. Mass fractal dimension values were slightly lower for dispersed-patch landscapes, but the slope of the response curves for both landscape patterns was the same.

4. Discussion

A meaningful interpretation of landscape metrics is only possible when the limitations of each measure are fully understood, the range of attainable values is known, and the user is aware of potential shifts in the range of values due to characteristics of landscape patches. It also is helpful to know whether a particular measure provides a unique contribution to our understanding of landscape structure and habitat fragmentation, or simply echoes the proportional representation of disturbance or the information provided by other measures.

Each of the metrics examined quantifies a component of landscape structure rather than providing a comprehensive, quantified summary. None of the measures is able to differentiate spatial patterns of patch dispersion, yet several measures provide information on other aspects of habitat fragmentation. In the following section, I describe the potential usefulness of each measure while highlighting drawbacks and limitations.

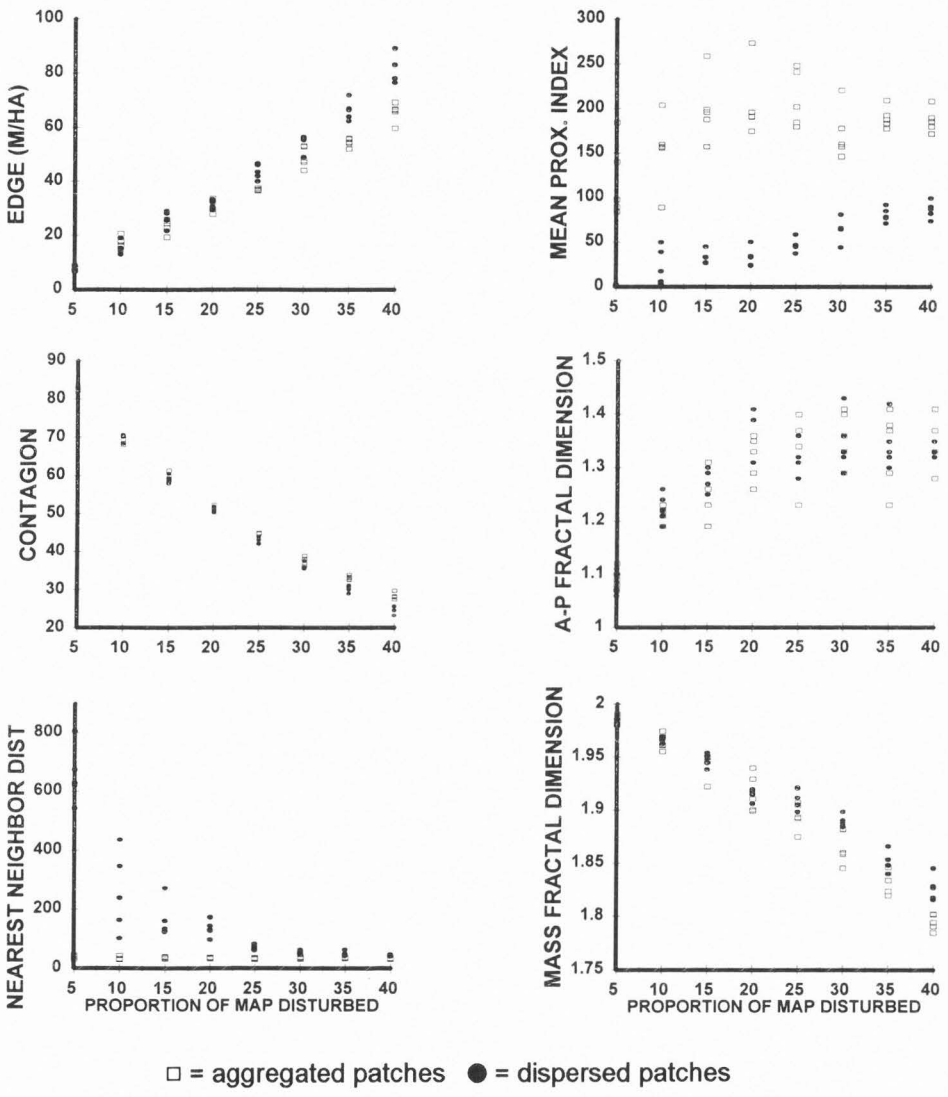


Fig. 2.8. Response curves for six landscape metrics on landscapes with either aggregated or dispersed patches.

4.1. Edge density

A primary outcome of habitat fragmentation is an increase in habitat edge, which is effectively quantified with edge density. This measure is entirely dependent on the ratio of patch area to patch edge, and landscapes with small patches or irregular shapes will have higher edge density values than landscapes with large patches or simple shapes at the same proportion of disturbance.

It is intuitive that edge density will increase with increasing representation of a disturbance cover type. However, if disturbance patches can coalesce or grow in size, edge density will eventually decline at successive levels of disturbance, because of the increase in patch area-to-edge ratio. As a consequence, both low- and high-disturbance landscapes have similar edge values, making it difficult to observe correlations between edge density and ecological phenomena over increasing disturbance. Many ecological questions are addressed over a narrow range of fragmentation, and duplicate values at different levels of disturbance generally are not a problem. Over narrow ranges, edge density is linearly correlated with change in the amount of disturbance, with the slope of the relationship determined by patch size and irregularity of patch edge.

Edge density is an effective tool for evaluating the effects of patch shape and area on the abundance of habitat edge. Wallin *et al.* (1994) used edge density to evaluate differences in dispersed versus aggregated timber harvest patterns, and found higher values with dispersed cutting. Since edge density is not sensitive to the spatial distribution of patches, the differences reported were due to differences in patch size used to create dispersed and aggregated harvest units rather than differences in harvest pattern.

4.2. Contagion

Contagion indices are designed to quantify the degree of aggregation found within cover types on a landscape (O'Neill *et al.* 1988; Li and Reynolds 1993). Contagion has been interpreted further to measure the interspersion of different patch types, as well as aggregation within a patch type (McGarigal and Marks 1995). I found, however, that contagion is insensitive to landscape patterns in which patches are either widely dispersed or clumped (Fig. 2.8). Even though a clumped disturbance produces a larger aggregation of original habitat (Fig. 2.4), there is no increase in contagion value compared to dispersed-patch landscapes.

The contagion index calculated by FRAGSTATS is based on the probability that an adjacent pixel differs in cover type from the current pixel. Changes in cover type occur at edges, and therefore, the contagion index is determined by the representation of edge pixels in a landscape. Rogers (1993) defines contagion as a measure of the frequency of occurrence of all possible edge types, a definition which highlights the association between contagion and edge. Both measures reflect the degree of aggregation within a cover type. When pixels of a cover type are highly aggregated, patches are large, relative to edge length, resulting in low values of edge and high values of contagion. Contagion is therefore determined by the ratio of patch area to patch edge in an inverse relationship with edge density, and the contagion value of a landscape will reflect the area:edge ratio of patches rather than the spatial arrangement of patches.

Since edge density and contagion provide the same information, use of both measures to quantify landscape pattern is redundant. Choice of measure depends on the

nature of the investigation. For example, the relationship between contagion and percolation theory (Gardner and O'Neill 1991) may seem intuitively easier to understand than edge and percolation theory, whereas habitat ecotones are best quantified by edge density (McGarigal and McComb 1995).

4.3. Mean nearest neighbor distance

Mean nearest neighbor distance provides information on spacing between patches in a cluster, a distance that grows exponentially shorter with increasing disturbance, regardless of the patch type or mode of disturbance growth (see also Gustafson and Parker 1992; Andrén 1994). When disturbance exceeds 0.20, this measure provides a range of values so narrow that discrimination among landscapes is difficult. However, the high variance in values when disturbance is < 0.20 suggests that it may be useful for differentiating inter-patch distances when fragmentation is low. Likewise, it could be used to assess distances between remnant patches of original habitat when disturbance is high.

The mean nearest neighbor distance measure is limited in applicability because it requires landscapes of similar extent and known grain for comparative studies. As with the other metrics examined, it also does not adequately describe the spatial distribution of patches. A landscape with all patches clumped can produce the same mean value as a landscape with widely dispersed pairs of patches (Rogers 1993). This difficulty can be somewhat overcome by reporting the standard deviation around the mean of the nearest neighbor distance, a statistic that can serve as a measure of patch dispersion (McGarigal and Marks 1995). However, the greatest shortcoming with mean nearest neighbor

distance is the inability to include the entire extent of a landscape in the calculations. The measure only applies to distances between patches in a cluster, ignoring the potentially vast distance between the edge of the cluster and the edge of the map (Fig. 2.4).

4.4. Mean proximity index

The proximity index is an effective measure of patch isolation for either remnant or disturbances patches. A notable property of this index is the radical change in values when the proportional representation of disturbance is around 0.55. At this point, there is a high probability that a single disturbance patch completely spans the map, reducing the nearest neighbor distance between all patches in the landscape, and greatly elevating mean proximity index values (Gustafson and Parker 1992).

The proportion at which a disturbance patch will completely span the landscape can be predicted by percolation theory, developed from a branch of physics that investigates the flow of particles or energy through a porous lattice of grid cells (Stauffer 1985). Assuming that flow can occur through only one of two possible cell types, the critical probability (P_c) of a substance percolating through an entire lattice occurs when the porous cells are connected in one continuous cluster. On an infinitely large lattice comprised of two randomly interspersed cell types, $P_c \approx 0.5928$ when clusters are formed through cell sides only, and $P_c \approx 0.4072$ if clusters can form through diagonal (corner) connections as well (Stauffer 1985).

On landscapes, percolation is the flow of any substance (fire, insects, species dispersal) through one of the landscape classes or cover types. The critical probability for

percolation, P_c, is approximated by the proportional representation of the "porous" cover type when a single patch of that cover type spans the entire landscape. Contagion broadens the critical probability to occur within a range of approximately 0.50-0.65 (Gardner and O'Neill 1991).

In my simulations, the actual point of percolation for cover type *j* is unknown because landscapes were generated at 0.10 intervals, but it occurs between 0.45-0.55. At this point, we observe a dramatic increase in both the values and variance of the mean proximity index, because interpatch distance, which serves as the denominator in the calculations, has been dramatically reduced by the existence of a spanning patch (Gustafson and Parker 1992). When disturbance growth is with buffered patches, the buffers restrict the disturbance from percolating, and the proximity index is truncated below the inflection point associated with percolation, creating a linear rather than sigmoid response curve (Fig. 2.7b).

Patch size affects the proximity index, since area is used in calculating this measure, yielding larger values for landscapes with larger patches (Fig. 2.7b). Slight differences in the spatial distribution of patches can substantially alter patch size. Shifting a patch location by one pixel can result in the coalescence of two small patches into one larger patch, substantially increasing the average area of all patches within the search radius. However, slight changes in the distance between patches have more effect than patch size. Shifting a patch so that the distance between it and a neighboring patch is a full pixel away rather than abutting diagonally will result in a substantial decrease in the proximity index, because the distance, and hence the denominator, is doubled (Gustafson and Parker 1992).

Use of the proximity index is best for disturbance levels below the critical probability for percolation. Above this, the wide range of observed values caused by slight differences in spatial arrangement of patches may be difficult to interpret ecologically. The proximity index can be applied where patches of interest occur in low densities and under different degrees of isolation, such as in gap analysis of species distribution and the study of spatial patterns of metapopulations. Spetich *et al.* (1995) used the proximity index to quantify the relative isolation of old-growth forest patches in Indiana. The proximity index would be an excellent tool in studies similar to that of Dunn *et al.* (1991). They compared isolated versus proximal woodlots in Wisconsin to examine the role of woodlot size and spatial distribution in the future dispersal of tree species.

4.5. Perimeter-area fractal dimension

The perimeter-area fractal dimension used in my simulations is one of several measures of fractal dimension used in the analysis of geographical data (Burrough 1986; Olsen *et al.* 1993). It is applicable when the ecological question is related to the irregularity of patch edges and the effect of this irregularity on landscape pattern, and has an advantage over edge density and other edge measures in that values derived are scale invariant.

This measure is essentially a patch-level statistic and will not differentiate between landscapes if all patches exhibit similar irregularity. In landscapes with buffered patches, the perimeter-area fractal dimension response curve was nearly flat across the range of increasing disturbance, because the average irregularity of individual patches did not

change with the placement of additional patches (Fig. 2.6). An example of this limitation is found in Ripple *et al.* (1991), where a comparison of two landscapes with buffered patches having similar edge shapes yielded perimeter-area fractal dimension values of 1.26 and 1.28, although disturbance increased from 8.5% to 23%.

By calculating perimeter-area fractal dimension for all patches in a landscape, the prime utility of this measure is lost, which is information on individual patch shape. The landscape average is a mid-range value between one and two that provides no information on landscape pattern and smooths the information pertaining to individual patch shapes. The range of possible values is further constrained by mapping techniques, because the fractal nature of patch edge is truncated by the resolution of the map and the tendency to simplify borders when patches are delineated.

Although perimeter-area fractal dimension has limited ability to quantify landscape pattern or fragmentation, it has greater applicability in our understanding of scaling relationships between landforms and ecological processes. For example, Milne (1994) used this measure to demonstrate the scaling relationship between coastline length of Admiralty Island, Alaska, and spacing of eagle nests along the coast, using data from Robards and Hodges (1976).

4.6. *Mass fractal dimension*

Mass fractal dimension has been used to quantify the configuration of landscape matrices created by patches. The shape of the mass fractal dimension response curve with increasing disturbance reflects the phenomenon of percolation, and most of the change in

fractal dimension values occurs after percolation of disturbance, as shown by the steepened response curve after $P_j = 0.55$, especially in landscapes with enlarging patches (Fig. 2.6).

Mass fractal dimension values are scarcely altered by size and shape of patches, as evidenced by similarity in response curves for all patch configurations (Fig. 2.6). I tested this conclusion by measuring mass fractal dimension on a series of maps constructed from randomly placed pixels in which I incrementally increased the proportional representation of one of the two pixel types at 0.10 intervals in the same manner as with the other simulations. Although the randomly placed pixels lack the inherent aggregation found in landscapes generated from predetermined patches, the response curve for mass fractal dimension derived from random pixel maps is similar to that of landscapes with overlapping patches, with values between 1.99-1.25. Thus, mass fractal dimension does not discriminate between landscapes containing random pixels and landscapes containing fairly large patches at the same level of disturbance.

Mass fractal dimension is highly correlated with increase in disturbance, resulting in correlation coefficients between -0.89 and -0.98 for the patch configurations and growth patterns that were simulated (Tables 2.1, 2.2, and 2.3). This finding, coupled with the inability to distinguish patterns of clumped versus dispersed patches, suggests that mass fractal dimension may have little utility for discriminating landscapes with differing sizes and shapes of patches at the size and scale illustrated here and frequently used by ecologists. As with perimeter-area fractal dimension, the strength of this measure may be in the investigation of scaling relationships between organisms and their environment.

Milne *et al.* (1992) used fractal geometry to characterize resource abundance at various scales, and investigated allometric relationships between three sizes of herbivores and fractally distributed resources. Ritchie and Moroge (in prep.) demonstrated that organisms viewing the environment on a large scale are more sensitive to habitat fragmentation than small-scale organisms, when the scaling relationship is considered from a fractal rather than Euclidean perspective.

5. Conclusion

Landscape metrics are developed to measure varying aspects of landscape structure, yet they are interrelated by their dependency on the same underlying measures of patch area, edge length, and inter-patch distance. In spite of the mathematical kinship, most measures I examined provide unique information about landscapes that is not contained in other metrics. The notable exceptions are contagion and edge density, which have near-perfect, inverse correspondence, because both measures are based on the proportion of edge pixels in a landscape. Perimeter-area fractal dimension also is related to contagion and edge density because of dependency on patch area and edge length in calculations. The correlation among all measures is greatest over disturbance levels < 0.40, because all measures except mean nearest neighbor distance exhibit the greatest linearity over this range.

None of the measures examined is sensitive to the spatial distribution of patches on a landscape. Mean nearest neighbor distance and mean proximity index both quantify distances between patches in a cluster, but neither is designed to place the cluster in the

context of the entire landscape. Edge density, contagion, and perimeter-area fractal dimension are all metrics of landscape pattern caused by size and shape of patches and their proportional representation on a landscape, but none can differentiate the spatial relationship among patches.

Ecologists using these measures can benefit by understanding the attainable values of each metric, and how these values are altered within landscapes characterized by different sizes and shapes of patches, and different modes of disturbance growth. I offer graphical representations of the attainable values derived from the simulations (Figs. 2.5, 2.6, 2.7, and 2.8) to assist ecologists in interpreting the values achieved for actual landscapes.

References

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71: 355-366.

Burrough, P.A. 1986. Principles of geographic information systems for land resources assessment. Oxford University Press, New York.

Dunn, C.P., Sharpe, D.M., Guntenspergen, G.R., Stearns, F. and Yang, Z. 1991. Methods for analyzing temporal changes in landscape pattern. *In* Quantitative methods in landscape ecology. pp.173-198. Edited by M.G. Turner and R.H. Gardner. Springer-Verlag, New York.

Forman, R.T.T. and Godron, M. 1986. Landscape ecology. John Wiley and Sons, New York.

Franklin, J. F. and R.T.T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecol. 1: 5-18.

Gardner, R.H. and O'Neill, R.V. 1991. Pattern, process, and predictability: the use of neutral models for landscape analysis. *In* Quantitative Methods in Landscape Ecology. pp. 289-307. Edited by M.G. Turner and R.H. Gardner. Springer-Verlag, New York.

Grossman, T. and Aharony, A. 1987. Accessible external perimeters of percolation clusters. J. Phys. A: Math Gen. 20: L1193-L1201.

Gustafson, E.J. and Parker, G.R. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. Landscape Ecol. 7: 101-110.

Kleinbaum, D.G., L.L. Kupper and K.E. Muller. 1988. Applied regression analysis and other multivariate methods. 2nd ed. PWS-Kent, Boston, Massachusetts.

Li, H. and Reynolds, J.F. 1993. A new contagion index to quantify spatial patterns of landscapes. Landscape Ecol. 8: 155-162.

Lord, J.M. and Norton, D.A. 1990. Scale and the spatial concept of fragmentation. Cons. Biol. 4: 197-202.

Lovejoy, S. 1982. Area-perimeter relation for rain and cloud areas. Science 216: 185-187.

McGarigal, K. and Marks, B.J. 1995. FRAGSTATS: Spatial analysis program for quantifying landscape structure. U.S. Forest Service Gen. Tech. Report PNW-GTR-351.

McGarigal, K. and McComb, W.C. 1995. Relationships between landscape structure and

breeding birds in the Oregon coast range. Ecol. Mon. 65: 235-260.

Milne, B.T. 1991. Lessons from applying fractal models to landscape patterns. *In* Quantitative methods in landscape ecology. pp. 199-235. Edited by M.G. Turner and R.H. Gardner. Springer-Verlag, New York.

Milne, B. T. 1994. Pattern analysis for landscape evaluation and characterization. *In* Eastside forest ecosystem health assessment. Vol. II: Ecosystem management: principles and applications. Pp 121-134. Edited by M. E. Jensen and P. S. Bourgeron. USDA Forest Service Gen. Tech. Rep. PNW-GTR-318.

Milne, B.T., Turner, M.G, Wiens, J.A. and Johnson, A.R. 1992. Interactions between the fractal geometry of landscapes and allometric herbivory. Theor. Pop. Biol. 41: 337-353.

Olsen, E.R., Ramsey, R.D. and Winn, D.S. 1993. A modified fractal dimension as a measure of landscape diversity. Photogrammetric Eng. and Remote Sensing 59: 1517-1520.

O'Neill, R.V., Krummel, J.R., Gardner, R.H, Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S. W., Dale, V.H. and Graham, R.L. 1988. Indices of landscape pattern. Landscape Ecol. 1: 153-162.

Ripple, W.J., Bradshaw, G.A. and Spies, T.A. 1991. Measuring forest landscape patterns in the Cascade Range of Oregon, USA. Biol. Cons. 57: 73-88.

Ritters, K. H., O'Neill, R. V., Wickham, J. D. And Jones, K. B. 1996. A note on contagion indices for landscape analysis. Landscape Ecol. 11:197-202.

Robards, F.C. and Hodges, J.I. 1976. Observations from 2,760 bald eagle nests in

southeast Alaska: progress report 1969-1076. Eagle management study. USDI Fish and Wildlife Service, Juneau, Alaska.

Rogers, C.A. 1993. Describing landscapes: indices of structure. M.S. Thesis, Simon Fraser University, Burnaby, British Columbia.

Spetich, M.A., Parker, G.R. and Gustafson, R.J. 1995. Spatial and temporal relationships of old-growth and secondary forests in Indiana. Proc. Tenth Annual Landscape Ecology Symposium, University of Minnesota, Minneapolis.

Spies, T.A., Ripple, W.J. and Bradshaw, G.A. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecol. Appl. 4: 555-568.

Stauffer, D. 1985. Introduction to percolation theory. Taylor and Francis, London.

Turner, M.G. 1990. Spatial and temporal analysis of landscape patterns. Landscape Ecol. 4: 21-30.

U.S. Department of Agriculture. 1982. National Forest System land and resource management planning. 36 CFR Part 219. Fed. Reg. 47: 43051.

Voss, R.F. 1984. The fractal dimension of percolation cluster hulls. J. Phys. A: Math. Gen. 17: L373-L377.

Voss, R.F. 1988. Fractals in nature: from characterization to simulation. *In* The science of fractal images. pp. 21-70. Edited by H.O. Peitgen and D.Saupe. Springer-Verlag, New York.

Wallin, D.O., Swanson, F.J. and Marks, B. 1994. Landscape pattern response to changes in pattern generation rules: land-use legacies in forestry. Ecol. Appl. 4: 569-580.

Whitcomb, R.F., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K. and

Bystrak, D. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. *In* Forest island dynamics in man-dominated landscapes. pp. 125-205. Edited by R.L. Burgess and D.M. Sharpe. Springer-Verlag, New York.

Wilcox, B.A. 1980. Insular ecology and conservation. *In* Conservation biology: an evolutionary-ecological perspective. pp. 95-117. Edited by M.E. Soulé and B.A. Wilcox. Sinauer Associates, Inc. Sunderland, Massachusetts.

CHAPTER 3

THE INFLUENCE OF FOREST FRAGMENTATION ON AMERICAN MARTEN POPULATIONS[1]

Abstract. I investigated the effects of forest fragmentation on American martens (*Martes americana*) by evaluating differences in marten densities across 18 study sites that varied in landscape heterogeneity due to the combined effects of natural openings and timber harvest clearcuts. The 9-km^2 sites were located in mature forests in the Uinta Mountains of northern Utah, and open areas occupied 2-42% of each site. I proposed three possible responses of marten populations to increases in fragmentation: 1) a linear negative decline based on habitat loss; 2) an initial positive response related to the added diversity and abundance of small mammals associated with clearcuts and meadows; and 3) an accelerated decline due to the combined effects of landscape pattern and habitat loss. I used ERDAS, a raster-based GIS, to classify the landscape images into 2-attribute maps representing forest and openings, and quantified fragmentation using five measures: the percent of each site in open areas, edge density, mean proximity index for open patches, mean nearest neighbor distance between open patches, and mass fractal dimension of the forest matrix. Within each site, I estimated marten abundance through live-trapping, estimated small mammal densities through snap-trapping, and collected data on forest structure. I found a significant negative correlation of marten captures to the combined effects of loss of forest habitat, as measured by the percent of each site in open areas and

---

[1]Coauthored by C. D. Hargis, J. A. Bissonette, and D. L. Turner.

an increase in the proportional representation of snags in the overstory ($P < 0.05$). The graphed relationship of marten captures and percent of site in openings suggested a possible threshold when open areas exceeded 20% of the landscape. Absence of martens occurred earlier than predicted by direct loss of habitat, implying additive effects of landscape pattern. Mean proximity index, which quantifies patch isolation based on the size and distance between open areas, was the strongest correlate with marten captures. Martens were not found in landscapes where patches were large and closely situated, and the combined effects of patch proximity and snag abundance explained more variation in marten captures than any other model examined ($R^2 = .59$). I found no evidence of a positive response to low levels of fragmentation. Small mammal densities were significantly higher in clearcuts than in forests ($P < 0.01$), but marten captures were not correlated with the increase in prey abundance or biomass associated with clearcuts. Conservation efforts for the marten must consider not only the structural aspects of mature forests, but the landscape pattern in which the forest occurs. I recommend that timber harvest blocks be aggregated to reduce forest edge and maintain maximum area in forest interior.

INTRODUCTION

The value of habitat to wildlife is influenced by landscape pattern. A landscape characterized by interspersion of patches provides essential habitat for species that use two or more habitat types, but has less value for species requiring large patches of unbroken habitat during part or all of their life histories (Whitcomb et al. 1981). Incremental

changes in landscape pattern cause habitat values to shift, becoming more favorable for certain species and less desirable for others, particularly through the process of fragmentation, when large tracts of an original cover type are gradually broken into smaller patches of two or more cover types or seral stages through human activities. Although fragmentation effects have received increased attention in recent years, the process through which habitat values change is poorly understood. Some animal populations may decline linearly with increasing fragmentation, whereas others may show no response until a critical threshold is reached. Other species may show positive responses to low levels of fragmentation and negative responses thereafter, whereas still others may increase across the entire fragmentation continuum.

The American marten (*Martes americana*), a carnivorous mammal associated with mature forest systems, appears sensitive to forest fragmentation, as evidenced by low populations in landscapes fragmented by the clearcut method of timber harvest (Soutiere 1979, Snyder and Bissonette 1987, Thompson and Harestad 1994). However, population responses to gradual increases in fragmentation are not well known. Current knowledge of marten biology could predict at least three possible responses: 1) a linear negative decline based on habitat loss; 2) an initial positive response related to the added diversity and abundance of small mammals associated with clearcuts and meadows; and 3) an accelerated decline due to the combined effects of landscape pattern and habitat loss (Fig. 3.1). With all three possible responses, there may be a critical threshold of fragmentation above which the landscape may not provide suitable habitat.

A linear negative response to fragmentation is one possible outcome, because

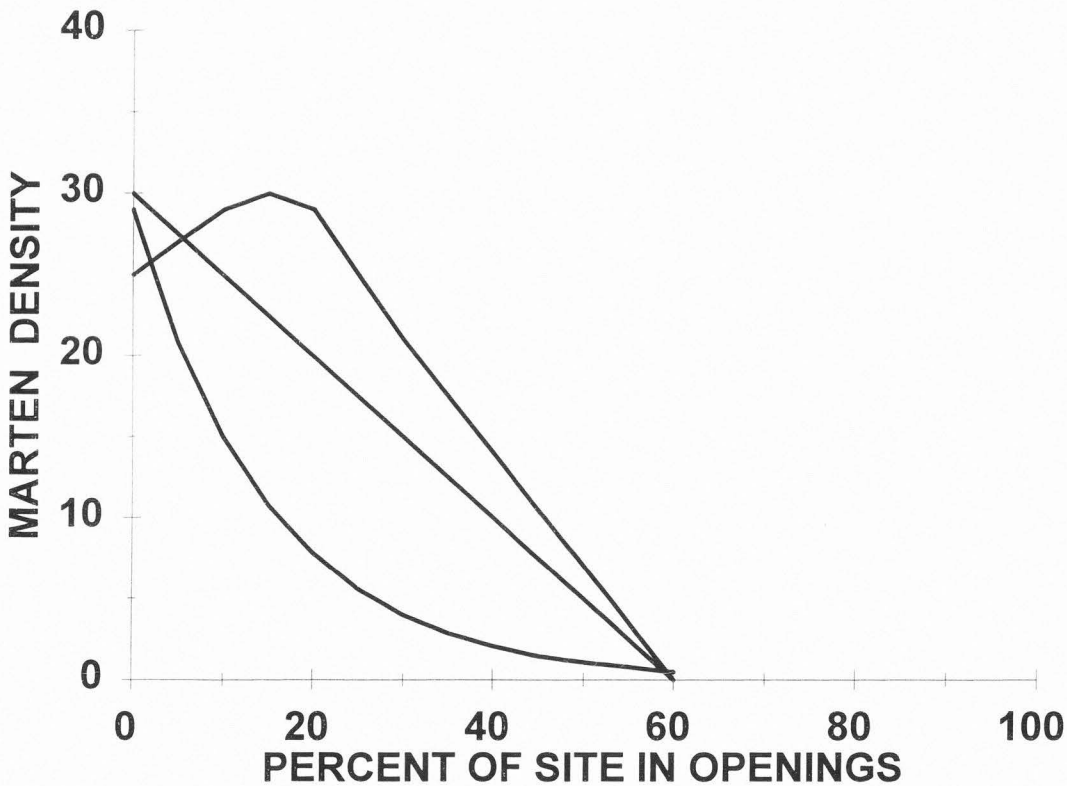


FIG. 3.1. Three predicted responses of marten populations to increasing fragmentation.

martens avoid clearcuts and other large openings, especially in the winter (Soutiere 1979, Clark and Campbell 1979, Steventon and Major 1982, Hargis and McCullough 1984). This behavior has been substantiated with baitbox experiments (Drew 1995). However, an initial positive response to fragmentation might also be expected because martens are known to forage in clearcuts during summer (Soutiere 1979) and to hunt along forest edges (Simon 1980, Spencer et al. 1983). They may respond positively to the increase in abundance and diversity of small mammmals associated with clearcuts, because their diets are not restricted to forest-associated prey (Weckwerth and Hawley 1962, Koehler and Hornocker 1977, Buskirk and MacDonald 1984). However, additional clearcuts eventually would cause population declines as forested habitat became limiting.

Regardless of the initial response, a threshold fragmentation level is expected when open areas are so prevalent that forest cover is no longer the landscape matrix. At this point, it would be necessary for martens to cross open areas to access desired forest patches.

With this threshold, loss of marten populations from habitat fragmentation could be predicted by percolation theory as applied to landscapes. Using a raster-based map comprised of pixels, let us assume that martens could move between forested pixels that are adjacent to one another or touch diagonally. On an infinitely large map of two randomly dispersed cover types, forest cover and open areas, martens would be able to move across the map without crossing an opening as long as the proportion of the map occupied by forest was greater than 0.41, which is the critical proportion below which the forest cover no longer would form a percolating cluster spanning the map (Stauffer 1985).

The critical proportion associated with percolation would vary for actual landscapes, depending on the degree of contagion caused by patch sizes and shapes, but still would be predictable based on probability curves generated for maps with various levels of contagion (Gardner and O'Neill 1991).

Marten populations may be sensitive to the spatial arrangement of patches rather than simply a shift in the proportion of forest cover to open areas. Landscape metrics that quantify the size and spatial arrangement of clearcut patches and the spatial configuration of the forest matrix may be more meaningful predictors of declines in marten numbers than simple proportions and percolation theory.

I undertook a study of fragmented, forested landscapes to investigate marten population responses to incremental increases in habitat fragmentation caused by the combined effects of natural openings and timber clearcuts. My first objective was to examine the response curve of marten density over increasing proportions of open areas, and look for specific levels of fragmentation that suggested shifts in habitat quality in either a positive or negative direction. Secondly, I wanted to determine whether a decrease in marten numbers was correlated with a simple loss of forest cover, or more specific changes in landscape configuration.

METHODS

I selected 18 sites in the Uinta Mountains of northern Utah that varied in the amount of open areas, ranging from 2-42% of each site (Fig. 3.2). Natural openings in the form of meadows and boulder fields covered 2-12% of the landscapes, while timber

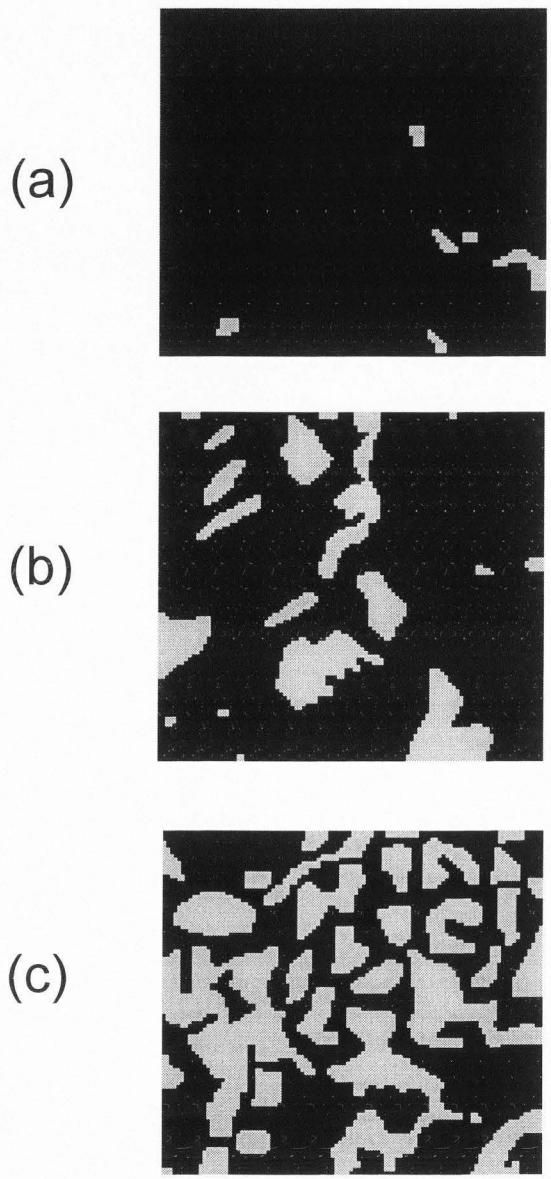


FIG. 3.2. Representative sites from the Uinta Mountains of northern Utah used in the study of forest fragmentation effects on the American marten: a) Beaver Meadow, least fragmented site with 2% of the site in natural openings; b) Hayden Pass, moderately fragmented with 17% of the site in clearcuts and natural openings; and c) East Park, most fragmented site, with 42% of the site in clearcuts, no natural openings.

harvests accounted for 0-42% of each site. The upper bound was close to the maximum possible because of the requirements for buffers between patches and legal constraints on patch size (≤ 16 ha) established by 36 CFR Part 219 (U.S. Dept. of Agriculture 1982) under the National Forest Management Act of 1976. I defined the borders of each site within a square area covering 9 km^2, a size selected to potentially encompass the territories of several martens, yet small enough to enable a thorough survey of the marten population.

To minimize sources of variation among sites due to factors other than fragmentation, all sites were located in mature forests containing Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and subalpine fir (*Abies lasiocarpa*), with canopy covers > 30%, large diameter trees, and abundant, large-diameter coarse woody debris. Elevations ranged from 2,700-3,200 m.

I chose sites with clearcuts at least 5 yr old to maximize the possibility of a stable marten population relative to this disturbance. Two sites contained additional clearcuts that had been harvested the previous year, but these totaled < 2% of each landscape. Most of the clearcuts had average tree heights < 2 m and were vegetated with grasses and forbs, providing a distinct contrast with adjacent forests.

This investigation involved four parts: a quantification of landscape fragmentation, estimation of marten density, estimation of potential prey density, and characterization of forest structure. The first two aspects were directly associated with the question of forest fragmentation effects on the American marten. The latter two assessed whether factors other than fragmentation explained observed differences in marten densities among sites.

Fragmentation analysis

I developed raster images of the study sites by extracting relevant areas from a vegetation map of the Uinta Mountains developed for a gap analysis of species distribution (Edwards et al. 1995). The map was derived from thematic mapper satellite data with 30-m pixel resolution and was classified to represent 35 vegetation types. Extracted study sites were 101 x 101 pixels and the vegetation types were aggregated into three attributes: forests, natural openings, and clearcuts. Natural openings were combined with clearcuts in the analysis of fragmentation.

I simplified the maps to reflect the scale at which martens appear to perceive their habitat. I assumed that martens would cross 30-m openings (Koehler and Hornocker 1977, Hargis and McCullough 1984), and reclassified isolated non-forested pixels and strips of non-forested habitat 30-m wide as forest. Likewise, isolated forest pixels embedded in an open polygon were reclassified to match the polygon.

Habitat fragmentation was quantified using five measures: the percent of landscape in openings, edge density (m/ha), mean proximity index, mean nearest neighbor distance between open areas (m), and mass fractal dimension. The first five measures were calculated with FRAGSTATS spatial pattern analysis program (McGarigal and Marks 1994). Mass fractal dimension was calculated using software developed by B. Milne and T. Keitt at the University of New Mexico, which they had included as an add-on toolbox within the Khoros image processing environment.

Percent of landscape in openings was the combined percentages of clearcuts and

natural openings within each study site, and represented loss of forest habitat. Edge density was the sum of all edge pixels divided by total landscape area and standardized as meters of edge per hectare.

Mean proximity index quantified the mean isolation of each open patch in the landscape from all other openings within a specified search radius, taking into account the size of all other openings as well as the distance among them. High values indicated closer proximity among open patches. I defined the length of the study site (3,000 m) as the search radius for each landscape. Proximity index for each patch was calculated as area of each patch divided by the square of the nearest edge-to-edge distance between it and the patch being indexed. Mean proximity index for each site was used as the landscape-level measure of average patch isolation (McGarigal and Marks 1994, modified from Gustafson and Parker 1992).

I also calculated mean nearest neighbor distance between openings as the average edge-to-edge distance between each nonforested patch in the landscape and its nearest neighbor. This measure differed from the proximity index by ignoring patch size and by defining inter-patch distance only with the nearest open patch. Mean nearest neighbor distance yielded an absolute value that only could be compared among sites of the same extent and resolution, whereas mean proximity index coud be used to compare landscapes of any extent, as long as the search radius and resolution were the same (Gustafson and Parker 1992).

Mass fractal dimension was used to describe the fractal nature of the forest matrix. I chose this fractal measure over a perimeter-area fractal because it characterized the

shape of the forest matrix caused by placement of open patches, whereas the perimeter-area fractal would have been more applicable if the intent were to measure the irregularity of individual patch perimeters. Mass fractal dimension was calculated from the scaling relationship between the average number of forested pixels within a subsample of the map and the length of the area defining the subsample (Voss 1988, Milne 1991). I delineated the subsamples within square boxes with edge lengths of 3, 9, 15, 21, and 27 pixels. Mean number of pixels per box was computed from the total number of forest pixels within all subsamples of a given box size centered on forest pixels, ignoring subsamples centered on open areas. Mass fractal dimension was the slope derived from the log of the average number of pixels associated with each box size regressed on the log of the box lengths (Voss 1988). Theoretical limits of this measure lie between 0-2. A value of 2 would be achieved if no open patches were present and the forest completely filled the 2-dimensional map space. As patches are added, the forest matrix would be reduced to some dimension < 2.

Marten density estimates

I estimated relative marten densities within each site through live-trapping in the summer. Twenty-five livetraps were placed in a systematic grid within each site and monitored for six consecutive nights, yielding 150 trap nights per site. Each of the 18 sites was sampled at least once during four trapping periods between 1991-1993. I resurveyed nine sites over 2 yr to examine potential differences in capture rates between years. One site was surveyed all three summers to indicate the magnitude of change in

capture rates over the entire span of the study. To examine potential differences in capture rates from early to late summer, I resurveyed four sites twice during the same summer.

Captured martens were sedated with ketamine, weighed, and ear-tagged. I determined gender and reproductive status of each individual and estimated age as either adult or juvenile based on development and wear of teeth.

I used relative marten density, expressed as the total number of individual martens captured per 100 trap nights, as a measure of habitat quality and the primary response to differences in fragmentation. To evaluate the usefulness of relative density as an indicator of habitat quality for martens (van Horne 1983, Pulliam 1988), I noted other habitat quality indicators, including evidence of reproductive activity, body weight and condition, and overwinter success, as determined by recaptures in subsequent years.

Marten populations were not subject to commercial harvesting. A 5-yr moratorium on commercial trapping of martens in the Uinta Mountains was initiated in 1990, one trapping season prior to the onset of my study. Additionally, no trappers engaged in trapping in 1988 or 1989 (Utah Division of Wildlife Resources, unpublished report).

Prey density estimates

I estimated small mammal populations within 12 of the sites during a 7-wk snap-trap survey between 22 July-8 September 1992. Each site was surveyed with 12 trap lines consisting of 16 stations spaced 20 m apart, with each station consisting of two mouse

traps and one rat trap. Lines were placed in forested areas, clearcuts, and meadows in approximate proportion to the availability of each of the three habitat types, and were run for two nights, yielding 1,200 trap nights per site. Actual trap nights were calculated by subtracting all traps that malfunctioned or were sprung each night.

I recorded the species, weight, and gender of each animal captured, and classed them as either juvenile or adult. Reproductive status of females was noted also. I estimated the relative abundance of each species using captures per 100 trap nights, and calculated total biomass of mammals per line based on measured weights. Data were summarized by site and by habitat types within each site.

Forest structure

I measured structural attributes of forested habitat using a modified plotless cruise at 25 points within each study site. Points were located at random compass directions and random distances between 1-30 m from each marten trap. At each point, I used a basal area prism to establish the number of trees included within the point sample, and recorded height, diameter (dbh), species, crown class, live crown ratio and snag decay class of each tree included.

I estimated the amount of conifer reproduction by tallying all trees < 7 cm dbh within four 2-m plots located five paces from each sampling point in the cardinal directions. Canopy cover was calculated with a densiometer at the center of these four plots.

I determined abundance of coarse woody debris using the inventory procedure

developed by Brown (1974). I established two 15-m transect lines that extended from the plotless cruise sampling point in random directions, and recorded the diameter of all woody material > 10 cm intersecting the lines. I classified woody debris as being either sound or rotten, and summarized the data as kg/ha for sound and rotten decay classes, using the calculations developed by Brown (1974).

Statistical analyses

At the end of the 3-yr survey period, I had surveyed each site one to three times out of four sampling periods. I used a bootstrap technique (Efron and Tibshirani 1993) to randomly generate 35 unique combinations of the four sampling periods, selecting one sampling period from each site. These combinations were used to form 35 data sets (n = 18) consisting of individual marten captures and total number of trap nights associated with each site.

I used Poisson regression analysis (Frome et al. 1973) to test for differences in marten capture rates among sites due to loss of habitat, landscape pattern, prey availability, and forest structure. I chose the Poisson model because marten captures were counts that occurred at a low rate, and the data most closely fit the Poisson distribution. The general form of the model was

individual captures/100 trap nights = f(fragmentation, prey, forest structure)

which can be expressed in a Poisson regression model as

$$\ln(C_i / T_i) = \beta_0 + \beta_1 F_i + \beta_2 P_i + \beta_3 S_i$$

where C = captures, T = 100 trap nights, F = fragmentation, P = prey availability, S =

forest structure, and β = regression coefficients. I used this general form to develop five specific fragmentation models, using the same prey and forest structure parameters in each, but varying the fragmentation term to be one of the five measures described in the section on fragmentation analysis. The prey and forest structure components of the model were selected from seven prey variables and 13 forest structure variables that appeared to differ among sites. I entered all 20 variables into a forward stepwise regression and selected one prey and one forest structure variable having the highest correlation with marten captures for incorporation as covariates into the fragmentation models.

Model parameters were estimated using maximum likelihood estimation (Kendall and Stuart 1946, Kleinbaum et al. 1988). The data were overdispersed, leading me to use a quasi-likelihood method of estimation, in which the degree of overdispersion was factored into the estimation of all statistics (McCullagh and Nelder 1991). For each of the six models, I compared the full model to a set of constrained models in which one of the three parameters was dropped. The criterion for a good fit was based on the change in model deviance between the full and reduced models, which is analogous to comparing regression sum of squares in linear regression analysis. The change in deviance between the full and reduced models followed a χ^2 distribution with $n - k - 1$ degrees of freedom (Frome et al. 1973, Kleinbaum et al. 1988). The likelihood ratio test statistic for change in model deviance was

$$D(\beta_r) - D(\beta_f) = -2 \ln\left[\frac{L(y;\beta_r)}{L(y;\beta_f)}\right]$$

where D = deviance, β = maximum likelihood estimators for reduced (r) and full (f) models, and L = maximized likelihood values of each model. I used the Wald χ^2 statistic, which is analogous to the likelihood ratio, but uses a contrast matrix rather than a series of likelihood ratios, and therefore requires less computation time (SAS Institute, Inc. 1993).

RESULTS

Marten response to fragmentation

Marten captures were negatively correlated with loss of habitat, as measured by the percent of each site in open areas (Fig. 3.3, Table 3.1). Capture rates were variable in sites with low fragmentation, but martens were rarely captured or absent in landscapes with > 0.21% open areas. I captured only one marten in 937 trap nights in the four sites having > 0.21% open areas.

These findings were based on captures of 53 individual martens (34 males and 19 females) in 4,983 trap nights within the summer seasons of 1991-93, with 0-8 individual captures per site during any given trapping period. I found no significant difference in capture rates between trapping periods ($\chi^2 = 2.89$, df = 3, $P = 0.41$). Sites with high captures were consistently high, and sites with zero captures remained low, resulting in a fairly stable ranking of sites across all years, and confirming that differences in capture rates were due to factors other than seasonal variation or sampling error.

Marten populations showed significant responses to landscape pattern as well as loss of habitat (Fig. 3.3, Table 3.1). Capture rates were lowest in landscapes with large,

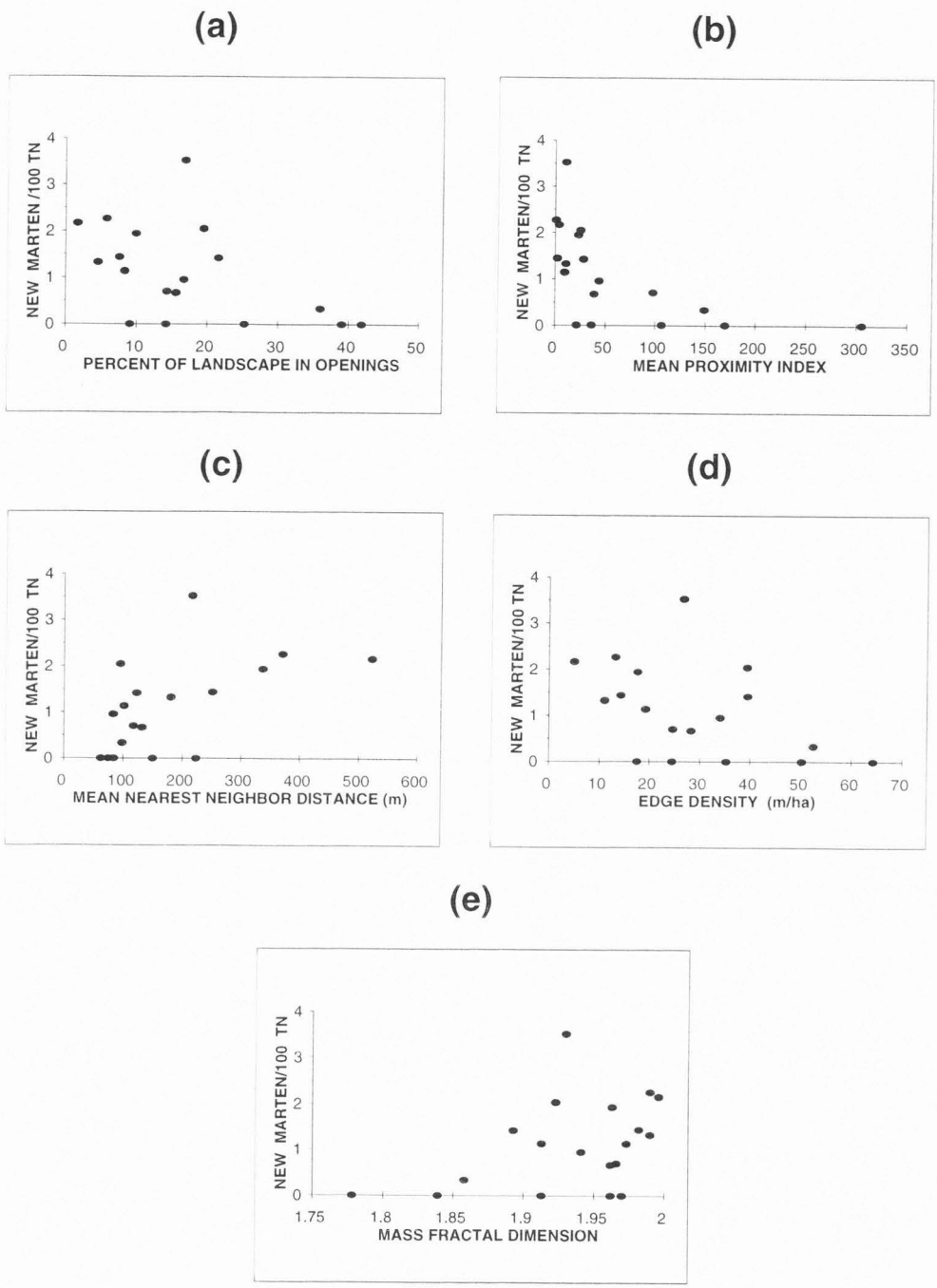


FIG. 3.3. Correlation of individual marten captures with five measures of fragmentation: a) percent of site in openings; b) mean proximity index; c) mean nearest neighbor distance; d) edge density; and e) mass fractal dimension.

TABLE 3.1. Statistical significance of models explaining individual marten capture rates, with mean *P*-values (confidence intervals in parentheses) derived from Wald chi-square tests performed on 35 bootstrap data sets per model (error df = 15 in each model).

Model parameters	*P*-value of fragmentation measure	*P*-value of snag abundance	R^2
Percent of site in openings	0.06 (0.05, 0.07)		0.23 (0.21,0.25)
Percent of site in openings, snag abundance	0.03 (0.02,0.04)	0.01 (0.01, 0.01)	0.50 (0.48,0.52)
Proximity index	0.01 (0.01, 0.01)		0.48 (0.47, 0.49)
Proximity index, snag abundance	0.04 (0.03, 0.05)	0.07 (0.06, 0.08)	0.59 (0.58, 0.60)
Nearest neigbor distance	0.03 (0.03, 0.03)		0.21 (0.20, 0.22)
Nearest neighbor distance, snag abundance	0.05 (0.02, 0.08)	0.03 (0.01, 0.05)	0.42 (0.40, 0.44)
Edge density	0.08 (0.07, 0.09)		0.19 (0.17, 0.21)
Edge density, snag abundance	0.05 (0.01, 0.09)	0.01 (0.00, 0.02)	0.47 (0.45, 0.49)
Mass fractal dimension	0.12 (0.10, 0.14)		0.17 (0.15, 0.19)
Mass fractal dimension, snag abundance	0.11 (0.04, 0.18)	0.02 (0.01,0.03)	0.43 (0.39, 0.47)

closely spaced open areas, as measured both by mean proximity index and nearest neighbor distance. Landscapes where the average distance between open areas was < 100 m had no marten captures. Also, landscapes with high edge density had fewer marten captures. I did not observe a significant correlation between marten captures and mass fractal dimension, although the trend was for low to zero captures in landscapes where the forest matrix was highly convoluted (Fig. 3.3, Table 3.1).

A qualitative assessment of population health indicated that marten density was an accurate estimate of habitat quality. The two sites with the highest captures were the only sites where I found evidence of overwinter success, based on captures in subsequent years. These sites also represented two of the four sites with lactating females, denoting reproductive activity. Although I found no correlation with mean adult male body weights and marten densities ($F = 0.332$, df = 1,9, $P = 0.58$), the average weight of males in the site with the highest captures was greater than the average for all sites. Also, body condition was fair to excellent in sites with high densities.

Influences of forest structure and prey

An examination of box and whisker plots for the forest structure parameters found 13 variables that differed sufficiently between sites to warrant inclusion in a forward stepwise regression to explain marten densities: average basal area (m^2/ha) of 1) all trees and 2) all live overstory trees; 3) total basal area; 4) basal area of the live overstory; average quadratic mean diameter (dbh_q) (cm) of 5) all overstory trees, 6) spruce, and 7) lodgepole pine; percent of the live overstory in 8) spruce and 9) lodgepole

pine; the abundance of snags, expressed as 10) the proportion of total trees and 11) the proportion of total overstory trees; 12) stand density index; and 13) canopy cover (%).

The forward stepwise regression also included information from the small mammal survey, which resulted in 1,753 captures over 11,417 trap nights, excluding sprung traps. The five most commonly trapped species were the southern red-backed vole (*Clethrionomys gapperi*), deer mouse (*Peromyscus maniculatus*), Uinta chipmunk (*Eutamias umbrinus*), least chipmunk (*Eutamias minimus*), and vagrant shrew (*Sorex vagrans*). Variables entered into the regression included captures/100 trap nights for each of these species, total biomass of captured mammals per site, and total captures/100 trap nights per site.

Snag abundance, as measured by the percent of total trees in snags, was the first variable entered into the model, explaining 30% of the variation in marten densities. The first prey variable entered was vole captures/100 trap nights, which explained 18% of the variation. Marten captures were negatively correlated with snag abundance and positively correlated with vole density (Fig. 3.4), and these two variables were selected for incorporation into the fragmentation models.

Vole density was ultimately dropped because of insignificance when a Poisson distribution for marten captures was assumed. Under the assumption of a normal distribution associated with stepwise regression, the correlation between marten captures and vole abundance was strengthened by high leverage from a site having both the highest marten captures and the second highest density of voles (Fig. 3.4). Most sites yielded two to four vole captures/100 trap nights, yet this site produced 11 captures/100 trap

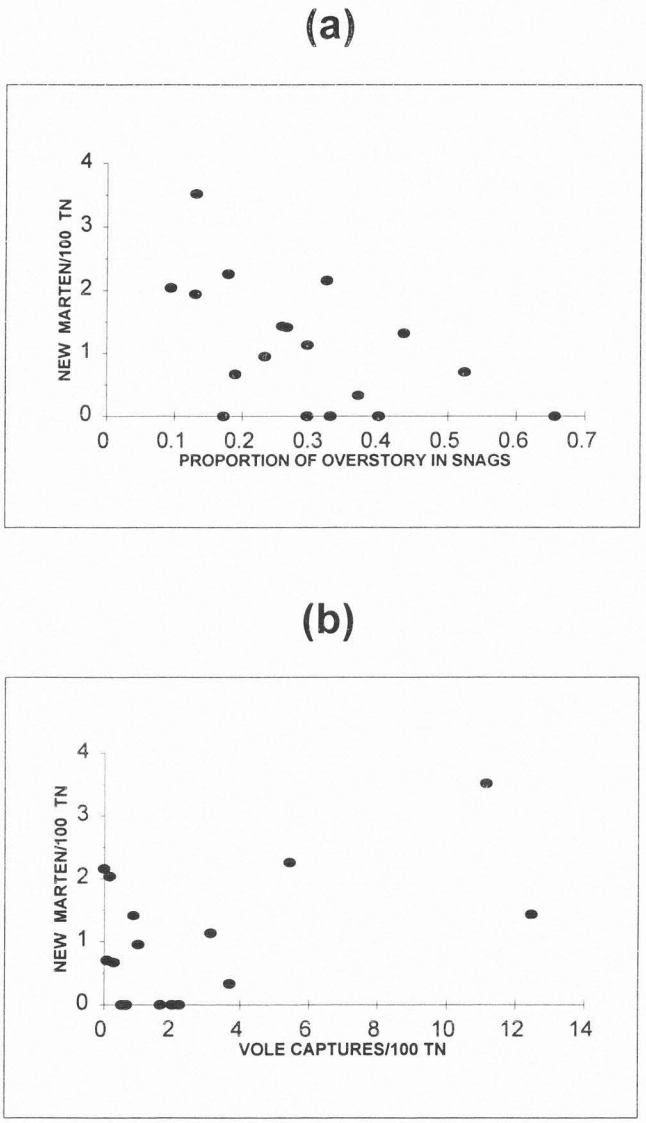


FIG. 3.4. Correlation of individual marten captures with a) proportion of snags in the overstory and b) vole captures/100 trap nights.

nights. When I assumed a Poisson distribution, vole abundance was not a significant predictor of marten captures, either when used alone (mean P of 35 bootstrap samples = 0.68, 95% CI = 0.65, 0.71) or in combination with one of the fragmentation measures and snag abundance (mean P of 35 bootstrap samples = 0.53, 95% CI = 0.50, 0.56).

Although none of the prey variables was significantly correlated with marten capture rates, differences in prey availability among forests, meadows, and clearcuts were useful in interpretation of marten response to fragmentation. Density of small mammals, based on captures/100 trap nights, was highest in clearcuts, followed by forests and meadows (Wald χ^2 for clearcuts versus forests = 20.12, df = 1, P = 0.001; Wald χ^2 for meadows versus forests and clearcuts = 16.14, df = 1, P = 0.001). I captured an average of 21 mammals/100 trapnights in clearcuts, 14/100 trap nights in forests, and 6/100 trap nights in meadows. Total biomass of all mammals captured, excluding snowshoe hares (*Lepus americanus*), was highest in clearcuts, followed by forests and meadows ($\underline{F}$ = 17.5, df = 2, $\underline{P} < 0.001$). Snowshoe hares (*Lepus americanus*) and red squirrels (*Tamiasciurus hudsonicus*) are known prey of martens (Hargis and McCullough 1984), but I was unable to acquire sufficient information on their abundance with snaptraps.

Comparison of fragmentation models

The combined effects of mean proximity index and snag abundance provided the best fit for explaining differences in marten capture rates, based on a comparison of P-values and R^2 terms from all fragmentation models examined (Table 3.1). The contribution of mean proximity index was greater than that of percent of site in openings,

which became an insignificant term when both measures were included in a model (mean P for each variable, respectively, based on 35 bootstrap runs = 0.37 and 0.01).

I examined correlations between percent of each site in openings and the four measures of landscape pattern to assess the degree of additional information provided by these measures (Table 3.2). Correlations were generally high, with mass fractal dimension having the highest correlation with habitat loss (r = -0.97) and nearest neighbor distance the lowest (r = -0.67). In addition, the four measures were interrelated among themselves, with edge density and mass fractal dimension having the strongest correlation (r = -0.96).

Partly as a consequence of these interrelationships, nearest neighhbor distance, edge density, and percent of site in openings were similar in their role as explanatory variables of marten capture rates. Used alone, each explained approximated 20% of the variation in marten capture rates and P-values were similar. When used in combination with snag abundance, percent of site in openings and edge density both became better predictors of marten captures, but the relationship between capture rates and nearest neighbor distance was weakened. Mass fractal dimension provided the poorest fit of all fragmentation measures examined, both when used alone or in combination with snag abundance.

DISCUSSION

Within the range of fragmentation examined, marten densities declined at a faster rate than expected from habitat loss alone, reflecting the additive effects of landscape

TABLE 3.2. Correlation matrix for variables used to investigate the response of marten density to fragmentation and snag abundance, with correlations between habitat loss (% open) and all other variables highlighted.

	Marten	% Open	Edge Density	Proximity Index	Nearest neighbor distance	Mass Fractal Dimension	Snags	Voles
Marten	1.000	-0.495	-0.454	-0.588	0.560	0.411	-0.534	0.499
% Open		1.000	0.973	0.852	-0.666	-0.970	0.276	-0.105
Edge			1.000	0.746	-0.728	-0.960	0.259	-0.156
Prox. Index				1.000	-0.500	-0.787	0.276	-0.190
Nearest neighbor dist.					1.000	0.586	-0.256	0.150
Fractal						1.000	-0.323	0.116
Snags							1.000	-0.274
Voles								1.000

pattern and snag abundance, and supporting my third prediction (Fig. 3.1). To illustrate this, I compared my data with two hypothetical responses that assumed a linear decline in marten densities from loss of habitat only (Fig 3.5). The hypothetical responses were generated by determining the number of individuals expected within 9-km^2 study sites, using two density estimates of 1.0 martens/km and 0.4 martens/km. I selected these estimates to fall within the same general range as densities observed in the least fragmented of my sites, and they are also similar to low and moderate densities reported for uncut forests in Ontario (Thompson and Colgan 1987, Thompson 1994). To compare my data with expected densities over increasing loss of habitat, I plotted the highest number of individuals captured within each site at each level of habitat loss represented by the 18 sites, and used a locally weighted smoothing function to graph a response curve through the data. Martens in my sites reached a density of zero early than expected from habitat loss alone, at a point when approximately three to six martens were predicted under low and high density estimates (Fig 3.5).

I found no evidence to support the prediction that martens would respond positively to low levels of fragmentation due to the increase in abundance and diversity of prey associated with increased landscape heterogeneity. Although small mammal densities were higher in clearcuts than in forest habitat, marten densities showed no positive correlation with the higher biomass of prey found in clearcuts, or with any species associated with clearcuts. The only relationship observed between marten densities and prey was with the red-backed vole, a species strongly associated with forest habitat (Raphael 1988). Within the Hayden Pass site, located at the west end of the Uinta

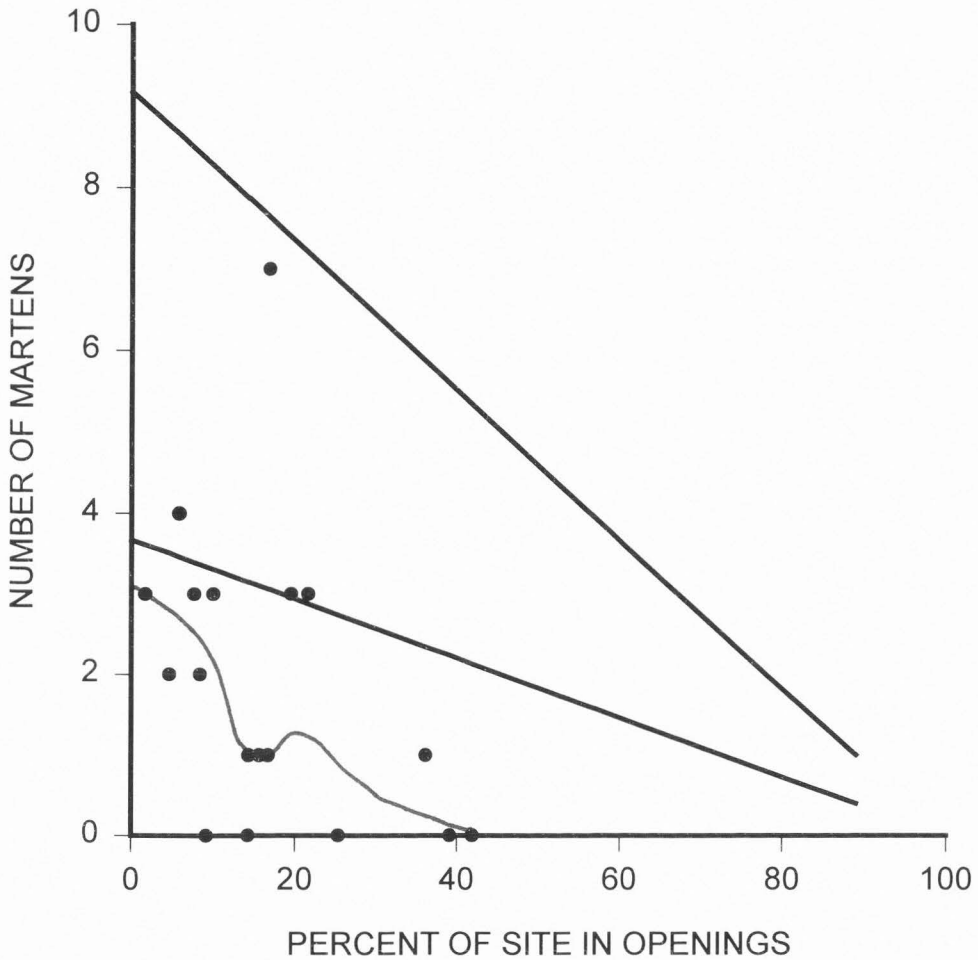


FIG. 3.5. A comparison of maximum number of martens trapped in 9-km^2 study sites in Utah with predicted numbers based on marten densities of 0.4/km^2 (lower line) and 1.0/km^2 (upper line).

Mountains (Fig. 3.2b), both marten and vole densities were notably higher than at all other sites. Hayden Pass was surveyed for martens during all 3 yr and consistently had the highest marten captures, but it ranked 12 out of the 18 sites in terms of available habitat, with 17% of the site in open areas. I attribute the high marten density to the abundance of prey in forest rather than clearcut habitat, particularly the abundance of red-backed voles, which were captured at three times the average rate for all sites during the Hayden Pass survey (Fig. 3.4).

The graphed response of marten density to loss of habitat could be interpreted as having a threshold at approximately 20%, since capture rates were variable among sites having 2-20% of the landscape in openings (Fig 3.3). However, the sample size is insufficient to conclude that a threshold is present, and the graphed relationship does not contain the interaction with snag abundance that I found to be significantly correlated with marten numbers. Regardless of whether the response to habitat loss was linear or exhibited a threshold, the general negative relationship is clear and presents a potential concern for marten population viability within moderately fragmented landscapes.

The point at which marten capture rates reached zero occurred earlier than predicted by percolation theory. Within all sites surveyed, the forest comprised the landscape matrix, and martens theoretically could travel across the landscape without having to enter an open area. This suggests that fragmented landscapes may become unsuitable to martens long before forest connectivity is lost.

The significant relationship between marten capture rates and mean proximity index indicates that martens are sensitive to both the size and proximity of open areas.

A mature forest may be rendered unsuitable for martens when the average nearest neighbor distance between open patches is < 100 m (Fig. 3.3). This pattern may be detrimental because of the lack of forest interior, which could affect several aspects of marten life history. Martens appear to utilize forest structure to avoid predators (Drew 1995), to gain access to prey in winter (Hargis and McCullough 1984, Buskirk and Powell 1994), and to gain thermal advantages, especially while resting (Buskirk et al. 1989), and each could be affected by proximity to forest edge. Paton (1994) determined that predation rates on birds near edges were most pronounced in the first 50 m from an opening, and if martens are vulnerable to predation, then forest patches <100 m wide would consist entirely of high-risk habitat between two open areas. Availability of preferred prey may also be a factor, since Mills (1995) found lower densities of California red-backed voles (*Clethrionomys californicus*) near edges than in forest interiors. If southern red-backed voles are influenced by edge also, then marten foraging success may be reduced in stands lacking interior habitat. Thermal advantages may also be lost along forest edges due to the more severe microclimatic conditions (Waring and Schlesinger 1985). These possible relationships suggest areas for further research.

In addition to probable edge effects, martens may not be able to utilize forests lacking interior due to the increased energetic costs of circumventing openings. It may be energetically prohibitive to defend a territory or forage in a home range that is widely diffused and interspersed with large patches of nonhabitat. There also may be increased predation risks. Regardless of the ultimate factors causing low to absent marten populations in landscapes lacking forest interior, these results indicate that conservation

efforts must consider not only the structural aspects of mature forests, but also the landscape pattern in which the forest occurs.

Snag abundance varied among sites more than any other component of forest structure due to differences in mortality from mountain pine beetle (*Dendroctonus ponderosae*) among sites. The representation of snags in the overstory ranged from 9% in a uninfected site to 65% in a heavily infected area. All other components of forest structure showed little variation because sites were all in mature forests with similar tree diameters, canopy cover, and coarse woody debris.

The negative correlation between snag abundance and marten capture rates partly reflects the relationship between martens and fragmentation, because timber sales are typically placed in beetle-infected stands to remove declining trees. I found a positive relationship between the percent of site in clearcuts and snag abundance ($F = 6.54$, df = 1,16, $P = 0.02$, $R^2 = 0.25$). The relationship between open areas and snag abundance was not significant when natural openings were included with clearcuts ($F = 1.32$, df = 1,16, $P = 0.27$, $R^2 = 0.02$). Therefore, snag abundance was only correlated with fragmentation due to clearcuts, not to the combination of clearcuts and natural openings.

I found no ecological explanations for the relationship between snag abundance and marten capture rates. High snag densities were correlated with low canopy cover ($F = 10.85$, df = 1,16, $P = 0.005$, $R^2 = 0.37$), but martens did not respond to the range of canopy covers observed among sites, which was between 28-55%. Also, I did not observe a correlation between the amount of coarse woody debris and snag abundance ($F = 0.15$, df = 1,16, $P = 0.70$, $R^2 = 0.0$), or between vole densities and snag abundance

($F = 1.29$, df = 1,16, $P = 0.27$, $R^2 = 0.02$). In Newfoundland, martens used snag-dominated stands because the open canopy resulted in a well-developed understory and higher densities of the principal prey for martens in that area, the meadow vole (*Microtus pennsylvanicus*) (Drew 1995, Sturtevant 1996). In contrast, red-backed voles in the Uinta Mountains showed no positive response to snag-dominated stands, and the data suggested a negative rather than positive trend in vole numbers with increasing snags.

Since snag abundance improved the fit of all fragmentation models (Table 3.1), it is more than a correlate with fragmentation, and must be influencing marten ecology in a way that my data did not reflect. I propose that edge effects may extend further into forests with high abundance of snags due to the more open canopy cover, causing a greater loss of forest interior at any given level of fragmentation than sites with low snag abundance.

The sensitivity to fragmentation I observed may appear more pronounced than reported elsewhere, due to the high contrast between forests and open areas in the Uinta Mountain sites. In Newfoundland, Snyder and Bissonette (1987) captured martens in residual forest patches < 24 ha in size that were isolated from larger patches of uncut forest, but adjacent clearcuts contained conifer regeneration and brush. Soutiere (1979) found martens using areas in Maine that were 60% cut, although at lower population levels than in uncut areas, and the cut areas were frequently well-vegetated with young conifers or deciduous shrubs that provided cover for martens during summer months. In my study sites, cut areas provided no cover, because I selected sites with the greatest contrast between open areas and forest habitat so that fragmentation effects could be

recognized easily. Typically, clearcuts were vegetated with conifers < 2 m in height and grasses, and most of the coarse woody debris had been piled and burned. The population response to fragmentation I observed may be more pronounced than observed in locations with rapid revegetation of cut areas, but could be expected in similar, high-contrast mosaics of managed timberlands throughout western North America.

Recommendations for management and research

Land managers have recognized that martens are strongly associated with mature forests, and have attempted to provide for this species by creating or retaining various components of forest structure. My study suggests that martens may be more sensitive to landscape pattern than previously acknowledged, and that high-contrast landscapes containing > 20% open areas, including natural openings as well as clearcuts, may not provide adequate marten habitat even when the matrix is mature forest and the desired structure is present. In addition to direct loss of habitat, martens appear sensitive to landscape patterns consisting of numerous openings separated by narrow forested buffers. I surmise that the unsuitability may be due to the increase in home range size brought about by large patches of nonhabitat, and/or the energetic costs of circumventing large openings while foraging, searching for mates, and marking territorial boundaries.

For conservation of forest interior species in managed landscapes, Franklin and Forman (1987) recommended progressive harvest of timber from scattered nuclei so that disturbance patches would be clustered and larger areas of undisturbed forest could be maintained. This recommendation would benefit martens because a greater portion of

forest would be in interior habitat. However, forested buffers left between tightly clustered clearcuts would have little value to martens, so they would represent additional loss of habitat.

A preferred strategy for preserving forest interior would be progressive cutting from a single patch, so that aggregation of cut blocks would be maximized, and the amount of high contrast edge minimized. Sequential, adjacent cut blocks would result in stairstep stages of regeneration across the entire patch. To illustrate the potential benefits to martens from clustered-patch and single-patch cutting patterns, I created two landscapes containing 20% open areas, the level of fragmentation above which martens were rarely found in my study, and placed the patches in a tight cluster or single aggregation. The simulations were done using a landscape fragmentation program developed by J. David and myself, which enabled us to place actual clearcuts from the Uinta Mountains on a forested landscape at any specified proportion and spacing. For a clustered-patch landscape, I specified that patches be no further than 90 m apart. For the single-patch landscape, I specified patches to overlap as they were placed. A comparison of the two simulations with an actual study site having 21% open areas illustrates the greater size of forest interior and fewer disruptions in continuity of habitat that could be created with clustered-patch or single-patch cutting patterns (Fig. 3.6).

Further insights into the effects of habitat fragmentation could be gained by investigating different patterns of patch placement at a specified percentage of open areas. I propose that landscapes with 20-35% open areas would offer the greatest opportunity to investigate the effects of landscape pattern on martens, because I observed a potential

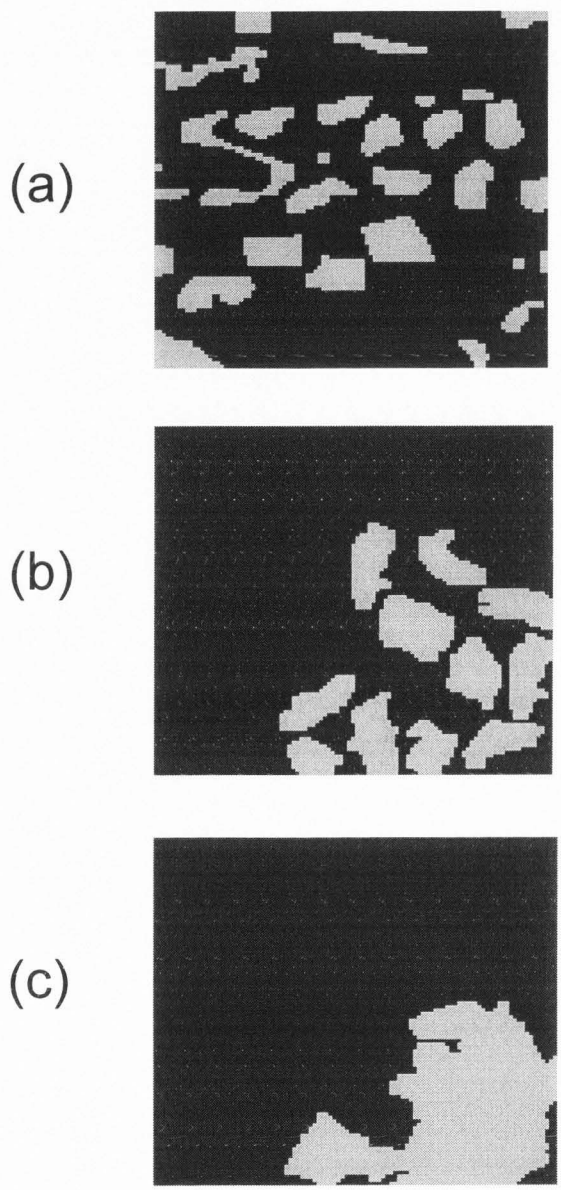


FIG. 3.6. Three landscape patterns with approximately 20% of the landscape in openings: a) an actual landscape in Utah; b) a simulated landscape with clustered patches; and c) a simulated landscape with clearcuts aggregated into a single patch to maximize forest interior.

threshold of habitat suitablity within this range. Also, more work is needed on edge effects within forested buffers between clearcuts, particularly regarding red-backed voles and other potential prey of martens. My study did not compare vole abundance between buffers and forest interior, but this comparison has the potential to provide an underlying mechanism for the lack of martens in fragmented landscapes. I also recommend research that would compare the effects of landscape heterogeneity from natural openings with that of anthropogenic fragmentation. In my study, these effects were combined. Lastly, more information is needed on the relationship between mountain pine beetle infestations, landscape fragmentation, and marten habitat, since beetle outbreaks are a major process affecting forest structure and landscape pattern in the western states.

LITERATURE CITED

Brown, J. K. 1974. Handbook for inventorying downed woody material. United States Department of Agriculture Forest Service General Technical Report **INT-GTR-16.**

Buskirk, S. W., S. C. Forrest, M. G. Raphael, and H. J. Harlow. 1989. Winter resting site ecology of marten in the central Rocky Mountains. Journal of Wildlife Management **53**:191-196.

Buskirk, S. W., and S. O. MacDonald. 1984. Seasonal food habits of marten in south-central Alaska. Canadian Journal of Zoology **62**:944-950.

Buskirk, S. W., and R. A. Powell. 1994. Habitat ecology of fishers and American martens. Pages 283-296 *in* S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R.

A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, New York, USA.

Clark, T. W., and T. M. Campbell. 1979. Population organization and regulatory mechanisms of pine martens in Grand Teton National Park, Wyoming. Pages 293-295 *in* R. M. Linn, editor. Conference on scientific research in national parks. Volume 1. National. Park Service Transactions and Proceedings Series 5, Washington, D. C., USA.

Drew, G. S. 1995. Winter habitat selection by American marten (*Martes americana*) in Newfoundland: why old growth? Dissertation. Utah State University, Logan, Utah, USA.

Edwards, T.C. Jr., C. G. Homer, S. D. Bassett, A. Falconer, R. D. Ramsey, and D. W. Wight. 1995. Utah gap analysis: an environmental information system. Utah Cooperative Fish and Wildlife Research Unit Technical Report **91-1**.

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, Inc., New York.

Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology **1**:5-18.

Frome, E. L, M. H. Kutner, and J. J. Beauchamp. 1973. Regression analysis of Poisson-distributed data. Journal of the American Statistical Association **68**:935-940.

Gardner, R. H., and R. V. O'Neill. 1991. Pattern, process, and predictability: the use of neutral models for landscape analysis. Pages 289-307 *in* M. G. Turner and R. H. Gardner, editors. Quantitative methods in landscape ecology. Ecological Studies

82. Springer-Verlag, New York, USA.

Gustafson, E. J., and G. R. Parker. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. Landscape Ecology 7:101-110.

Hargis, C. D., and D. R. McCullough. 1984. Winter diet and habitat selection of marten in Yosemite National Park. Journal of Wildlife Management **48**:140-146.

Kendall, M. G., and A. Stuart. 1946. The advanced theory of statistics, volume 2. Hafner Publishing Company, New York, USA.

Kleinbaum, D. G., L. L. Kupper, and K. E. Muller. 1988. Applied regression analysis and other multivariable methods. PWS-Kent Publishing Company, Boston, Massachusetts, USA.

Koehler, G. M., and M. G. Hornocker. 1977. Fire effects on marten habitat in the Selway-Bitterroot Wilderness. Journal of Wildlife Management **41**:500-505.

McCullagh, P., and J. A. Nelder. 1991. Generalized linear models. Chapman and Hall, New York, USA.

McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: Spatial analysis program for quantifying landscape structure. United States Department of Agriculture Forest Service General Technical Report **PNW-GTR-351.**

Mills, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. Conservation Biology 9:395-403.

Milne, B. T. 1991. Lessons from applying fractal models to landscape patterns. Pages 199-235 *in* M. G. Turner and R. H. Gardner, editors. Quantitative methods in landscape ecology. Springer-Verlag, New York, USA.

Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology **8**:17-26.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist **132**:652-661.

Raphael, M. G. 1988. Habitat associations of small mammals in a subalpine forest, southeastern Wyoming. Pages 359-366 *in* R. C. Szaro, K. E. Severson, and D. R. Patton, technical coordinators. Management of amphibians, reptiles, and small mammals in North America. United States Department of Agriculture Forest Service General Technical Report **RM-GTR-166.**

SAS Institute, Inc. 1993. SAS/STAT Software: The GENMOD procedure, release 6.09. SAS Technical Report P-243, SAS Institute, Inc., Cary, North Carolina, USA.

Simon, T. L. 1980. An ecological study of the marten in the Tahoe National Forest, California. Thesis. California State University, Sacramento, California, USA.

Snyder, J. E. and J. A. Bissonette. 1987. Marten use of clear-cuttings and residual forest stands in western Newfoundland. Canadian Journal of Zoology **65**:169-174.

Soutiere, E. C. 1979. Effects of timber harvesting on marten in Maine. Journal of Wildlife Management **43**:850-860.

Spencer, W. D., R. H. Barrett, and W. J. Zielinski. 1983. Marten habitat preferences in the northern Sierra Nevada. Journal of Wildlife Management **47**:1181-1186.

Stauffer, D. 1985. Introduction to percolation theory. Taylor and Francis, London, United Kingdom.

Steventon, J. D., and J. T. Major. 1982. Marten use of habitat in a commercially clear-

cut forest. Journal of Wildlife Management **46**:175-182.

Sturtevant, B. R. 1996. Second growth forest as potential marten habitat in western Newfoundland: an examination of forest habitat structure and microtine abundance. Thesis. Utah State University, Logan, Utah, USA.

Thompson, I. D. 1994. Marten populations in uncut and logged boreal forests in Ontario. Journal of Wildlife Management **58**:272-279.

Thompson, I. D., and P. W. Colgan. 1987. Numerical responses of marten to a food shortage in north-central Ontario. Journal of Wildlife Management **51**:824-835.

Thompson, I. D., and A. S. Harestad. 1994. Effects of logging on American martens, and models for habitat management. Pages 355-367 *in* S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, New York, USA.

U. S. Department of Agriculture. 1982. National Forest System land and resource management planning. 36 CFR Part 219. Federal Register **47**:43051.

van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management **47**:893-901.

Voss, R. F. 1988. Fractals in natures: from characterization to simulation. Pages 21-70 *in* H. O. Peitgen and D. Saupe, editors. The science of fractal images. Springer-Verlag, New York, USA.

Waring, R. H., and W. H. Schlesinger. 1985. Forest ecosystems: concepts and management. Academic Press, Inc., Orlando, Florida, USA.

Weckwerth, R. P., and V. D. Hawley. 1962. Marten food habits and population

fluctuations in Montana. Journal of Wildlife Management **26**:55-74.

Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-205 *in* R. L. Burgess and D. M. Sharpe, editors. Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, USA.

CHAPTER 4

LANDSCAPE-LEVEL EFFECTS OF TIMBER HARVESTS ON SMALL-MAMMAL POPULATIONS IN SPRUCE-FIR FORESTS[1]

Abstract

Small-mammal communities are affected by changes in vegetation and habitat structure resulting from clearcut timber harvests, but the effects of multiple clearcut blocks at the landscape scale have not been studied. I conducted a small-mammal survey within a series of 9-km^2 landscapes containing varying proportions of forest and open areas to examine effects of landscape pattern on small-mammal populations. The broad scale of this study also provided a large and geographically disjunct set of clearcut blocks and forest stands for comparing small-mammal communities between these habitats. I surveyed small-mammal populations over a 7-week period between 22 July and 8 Sept 1992, using 1,200 trap nights per study site, and captured 14 species of small mammals. The five most commonly trapped species were the southern red-backed vole (*Clethrionomys gapperi*), deer mouse (*Peromyscus maniculatus*), Uinta chipmunk (*Eutamias umbrinus*), least chipmunk (*Eutamias minimus*), and shrew (*Sorex spp*). Capture rates of southern red-backed vole, the most frequently captured species in mature forests, declined with loss of forest habitat, but the decline was greater than predicted

---

[1]Coauthored by C. D. Hargis and J. A. Bissonette

from a null model of capture rates based on habitat loss alone. Landscape pattern appeared to serve as an additive effect contributing to lower captures of red-backed voles in landscapes with high edge density, little forest interior, and large, open areas in close proximity. In contrast, these landscape patterns were associated with increased capture rates of deer mice, which occurred in greatest numbers in clearcuts and in landscapes with high juxtaposition of open areas with forests. The Uinta chipmunk was the only other species captured in sufficient numbers to analyze statistically, and I found no change in capture rates with fragmentation. At the scale of individual cut blocks and habitat comparisons, I found greater species richness in mature forests, but higher overall capture rates in clearcut blocks. I concluded that land managers must be aware not only of the effects of individual cut blocks, but of the larger scale effects of cut blocks on landscape pattern and small mammals, as well as the potential influences on larger species for whom the small mammals serve as prey. I recommend aggregated rather than dispersed patterns of clearcuts so that a greater proportion of the landscape can be maintained in forest interior habitat for species that are sensitive to habitat area and edge.

1. Introduction

Clearcut timber harvest methods change the vegetative cover of cut areas from mature conifers to an early seral stage dominated by grasses, forbs, shrubs, and young trees. Effects of clearcutting on small mammals have been investigated by comparing species occurrences and abundance within the original cover type and in various seral stages of the clearcut blocks, using either snap-trapping (Ramirez and Hornocker 1981;

Gunther *et al.* 1983) or live-trapping surveys (Gashwiler 1970; Petticrew and Sadleir 1974; Scrivner and Smith 1984; Walters 1991).

Although studies have documented substantial differences in small-mammal populations between clearcuts and mature forests, little is known about small-mammal responses to clearcutting at a larger spatial scale where the number and placement of cut areas defines the configuration of the landscape. The small size and limited foraging range of most small mammals relative to clearcut patch size suggest that a response to large-scale patterns is unlikely. However, there is evidence that southern red-backed voles (*Clethrionomys gapperi*) and California red-backed voles (*Clethrionomys californicus*) are less abundant at forest-clearcut edges (Walters 1991; Mills 1995), implying a possible sensitivity to landscape pattern.

I conducted a small-mammal survey at the landscape scale to investigate small-mammal responses to landscape pattern created by clearcut blocks. This survey was part of a study conducted to investigate effects of landscape pattern on the American marten (*Martes americana*). My approach was to test for differences in marten and small-mammal abundances within a series of equal-sized forested landscapes containing varying proportions of clearcut patches.

In addition to investigating effects of landscape pattern, the large scale of this study enabled me to repeat the forest-clearcut comparisons of past studies, but with a larger sample size than previously reported. With few exceptions (Ramirez and Hornocker 1981), former studies have compared a single cut block or neighboring cut blocks to a single stand of the original cover type (Gashwiler 1970; Petticrew and Sadleir

1974; Gunther *et al.* 1983; Scrivner and Smith 1984; Walters 1991). Because of the lack of replicates, it is not possible to discern local variation within a study from actual differences in small-mammal responses between studies.

This is problematic, because findings are not in agreement. For example, Petticrew and Sadleir (1974) found no difference in the abundance and survival of deer mice (*Peromyscus maniculatus*) between mature forest, recently logged, and young plantation habitats, whereas Scrivner and Smith (1984) found significantly more deer mice in older seral stage stands, and Ramirez and Hornocker (1981) found significantly higher densities in 5-yr-old clearcuts. Comparing abundance patterns of red-backed voles (*Clethrionomys gapperi*), Ramirez and Hornocker (1981) found greater densities in uncut forests, Gunther *et al.* (1983) found greater densities in clearcuts, and Walters (1991) found no difference between uncut forests and unburned clearcuts.

The broad geographic coverage of my landscape-level study resulted in small-mammal survey lines within numerous clearcut and forest stands that were useful for replications at the scale of the individual cut block or stand. In this chapter, I present findings on small-mammal responses at two spatial scales: 9-km^2 landscapes consisting of numerous cut blocks, and the scale of the individual cut blocks.

2. Methods

I selected 12 sites in the Uinta Mountains of northern Utah, each covering 9 km^2 and containing mature forests with varying amounts of landscape heterogeneity from clearcut harvest activity and natural openings in the form of meadows, boulder fields, and

occasional lakes. The proportion of clearcut patches within each landscape ranged from 0-31%, and the combined proportion of clearcut blocks and natural openings ranged from 6-39% (Fig. 4.1). The upper end of the range approached the maximum fragmentation possible, because all sites were on USDA Forest Service lands with legal constraints on the size of individual cut blocks (≤ 16 ha) and requirements for buffers between cut blocks established by 36 CFR Part 219 (1982) under the National Forest Management Act of 1976 (U.S. Dept. of Agriculture 1982). The sites covered the entire extent of the Uinta Mountains, with 3-100 km between sites.

To minimize sources of variation among sites caused by factors other than landscape pattern, all sites were located between elevations of 2,700-3,200 m in mature forests of Engelmann spruce (*Picea engelmannii*) and lodgepole pine (*Pinus contorta*) with canopy cover generally > 30%. Subalpine fir (*Abies lasiocarpa*) was also present in most sites. The dominant ground cover was grouse whortleberry (*Vaccinium scoparium*), and most stands contained abundant, large-diameter, woody debris. Clearcuts were vegetated predominantly with grasses, forbs, and conifers < 2 m in height, creating high contrast with adjacent forests. Clearcuts lacked woody structure, because logging slash was typically piled and burned.

I selected sites in which the age of the majority of clearcuts was > 5 yr to increase the likelihood that small-mammal populations had stabilized relative to the disturbance. However, timber activity was still in progress in some areas. One site had clearcuts < 2 yr old, while two other sites contained clearcuts harvested the previous summer. New

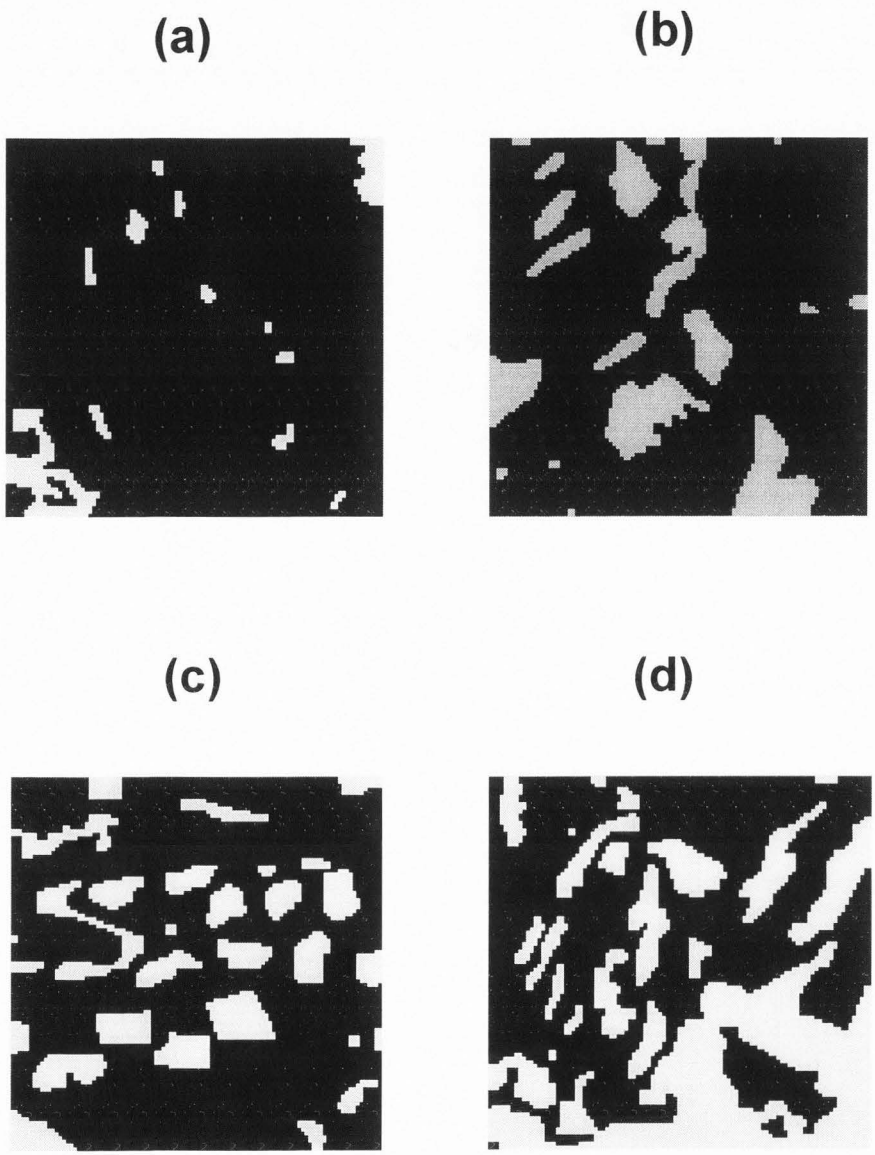


Fig. 4.1. Four of the 9-km^2 landscapes from the Uinta Mountains of northern Utah selected for the study of landscape-level effects of clearcuts on small mammal populations: a) least fragmented site, 6% in openings and 82% in forest interior; b) 18% in openings and 65% in forest interior; c) 22% in openings and 53% in forest interior; and d) most fragmented site, 39% in openings and 36% in forest interior.

harvest blocks within these latter sites represented < 3% of total clearcuts within each landscape.

Forest fragmentation was measured in four ways: 1) percent of each site in open areas; 2) percent of forest interior habitat within each site, based on a 60-m edge width; c) mean proximity index, a measure of patch isolation; and 4) edge density, expressed as meters of high contrast forest edge/ha.

Mean proximity index quantified the mean isolation of each open patch in the landscape from all other openings within a specified search radius, taking into account the size of all other openings as well as the distance among them (Whitcomb *et al.* 1981; Gustafson and Parker 1992). High values indicated closer proximity among open patches. I used the length of the study site (3,000 m) as the search radius for the proximity index of each patch. Proximity index for each patch was calculated as area of each patch divided by the square of the nearest edge-to-edge distance between it and the patch being indexed. Mean proximity index for each site was used as the landscape-level measure of average patch isolation (McGarigal and Marks 1995, modified from Gustafson and Parker 1992).

The measures were calculated from raster images of the study sites based on thematic mapper data with 30-m pixel resolution, obtained by extracting relevant portions from a GAP analysis vegetation map of Utah (Edwards *et al.* 1995). I collapsed 37 vegetation types of the original map into three attributes: forest, natural openings, and clearcuts, and further simplified the landscape patterns by reclassifying all single-pixel patches to match the surrounding attribute. Thus, isolated nonforested pixels were reclassified as forest, and solitary forest pixels embedded in a clearcut or meadow polygon

were reclassified to match the polygon (Fig. 4.1). I combined natural openings and clearcuts when calculating the percent of each site in open areas. To obtain forest interior values, I delineated a 60-m (2-pixel) edge buffer around all forest polygons and summed the forest core areas for each site using the FRAGSTATS spatial pattern analysis program (McGarigal and Marks 1995).

I surveyed small-mammal populations over a 7-wk period between 22 July and 8 September 1992, with sites sampled in random sequence. Each site was surveyed with 12 trap lines consisting of 16 stations spaced 20 m apart, with each station consisting of two mouse traps and one rat trap. Lines were placed in forested areas, clearcuts, and natural openings in approximate proportion to the availability of each of the three habitat types, and were run for two nights, yielding 1,200 trap nights per site. I monitored six lines at a time and spent four consecutive nights at each site. Actual trap nights were calculated by subtracting all traps that malfunctioned or were sprung each night.

Traps were checked in early morning and late afternoon to maximize captures of both diurnal and nocturnal species, and to minimize loss of captures to scavengers. However, sprung traps were not reset between morning and afternoon checks, and the two periods were considered one trapping effort. I recorded species, weight, and gender of each animal captured, and noted the reproductive status of females. I estimated age as either juvenile or adult based on weight and pelage color.

I estimated the relative abundance of each species using captures per 100 trap nights, and calculated biomass per trap line based on measured weights. I calculated species diversity for each trap line using the Shannon-Weaver (Shannon and Weaver

1949) and Simpson's (Simpson 1949) diversity indices.

I used Poisson regression analysis (Frome *et al.* 1973) to examine differences in capture rates across the range of fragmentation and between habitats (forests, clearcuts, and meadows). I chose the Poisson model because small-mammal captures were counts that occurred at a low rate relative to the trapping effort, and the data most closely fit the Poisson distribution. The general form of the model was

$$\text{captures/100 trap nights} = f(\text{fragmentation, habitat})$$

which can be expressed in a Poisson regression model as

$$\ln(C_i / T_i) = \beta_0 + \beta_1 F_i + \beta_2 H_i$$

where C = captures, T = 100 trap nights, F = fragmentation, β = regression coefficients. I used this general form to develop a series of models for each of the most commonly trapped species, using one of the four measures of fragmentation in each model.

Model parameters were estimated using maximum likelihood estimation (Kendall and Stuart 1946; Kleinbaum *et al.* 1988). The data were overdispersed, leading me to use a quasi-likelihood method of estimation, in which the degree of overdispersion was factored into the estimation of all statistics (McCullagh and Nelder 1991). For each statistical test, I compared a full model containing both fragmentation and habitat to a reduced model in which one of the parameters was removed. The criterion for a good fit was based on the change in model deviance between the full and reduced models, which is analogous to comparing regression sum of squares in linear regression analysis. The change in deviance between the full and reduced models followed a χ^2 distribution with $n - k - 1$ degrees of freedom (Frome *et al.* 1973; Kleinbaum *et al.* 1988). The likelihood ratio

test statistic for change in model deviance was

$$D(\beta_r) - D(\beta_f) = -2 \ln\left[\frac{L(y;\beta_r)}{L(y;\beta_f)}\right]$$

where D = deviance, β = maximum likelihood estimators for reduced (r) and full (f) models, and L = maximized likelihood values of each model. I used the Wald χ^2 statistic which is analogous to the likelihood ratio, but develops a contrast matrix rather than a series of likelihood ratios, and therefore requires less computation time (SAS Institute, Inc. 1993). R^2 values were derived from the ratio of model deviance to total deviance, similar to the ratio of regression sum of squares to total sum of squares used in generalized regression models.

For all variables other than capture rates (the two diversity indices and trap line biomass), I assumed a normal distribution of the response variable. With both Poisson and normal models, I examined the effects of habitat and fragmentation simultaneously, and when fragmentation was not significant, I reduced the model and tested for habitat effects alone. Thus p-values reported for habitat effects are from multivariate models when fragmentation was significant, but otherwise are from univariate models. I found no models in which fragmentation was significant and habitat was not.

3. Results

I captured 14 species of small mammals, excluding the incidental capture of a short-tailed weasel (*Mustela erminea*) (Table 4.1). All 14 species were captured in forest

Table 4.1. Small-mammal captures/100 trap nights by habitat (and total captures) within three habitats surveyed in the Uinta Mountains of northern Utah.

Species	Forests		Clearcuts		Meadows	
Red-backed vole (*Clethrionomys gapperi*)	5.6	(414)	0.7	(18)	0.3	(3)
Least chipmunk (*Eutamias minimus*)	0.2	(14)	2.4	(65)	0	(0)
Uinta chipmunk (*Eutamias umbrinus*)	1.7	(128)	1.7	(48)	0.2	(2)
Flying squirrel (*Glaucomys sabrinus*)	0.1	(11)	0	(0)	0	(0)
Snowshoe hare (*Lepus americanus*)	0.1	(7)	< 0.1	(1)	0	(0)
Long-tailed vole (*Microtus longicaudus*)	0.1	(7)	0.1	(3)	0	(0)
Montane vole (*Microtus montanus*)	< 0.1	(1)	0.1	(2)	0.5	(5)
Deer mouse (*Peromyscus maniculatus*)	4.9	(361)	15.3	(420)	3.9	(41)
Heather vole (*Phenacomys intermedius*)	< 0.1	(2)	0	(0)	0.7	(7)
Masked/vagrant shrew (*Sorex cinereus/vagrans*)	1.0	(75)	0.6	(17)	1.0	(11)
Water shrew (*Sorex palustris*)	< 0.1	(1)	0	(0)	0	(0)
Golden-mantled gr. squirrel (*Spermophilus lateralis*)	<0.1	(3)	0.8	(22)	0	(0)
Red squirrel (*Tamiasciurus hudsonicus*)	< 0.1	(4)	0	(0)	0	(0)
W. jumping mouse (*Zapus princeps*)	< 0.1	(4)	0	(0)	0.1	(1)

habitat, nine species were captured in clearcuts, and seven in meadows. I captured 1,698 animals over 11,183 trap nights, for a rate of 15.2 captures/100 trap nights.

The five most commonly trapped species were the southern red-backed vole, deer mouse, Uinta chipmunk (*Eutamias umbrinus*), least chipmunk (*Eutamias minimus*), and shrew (*Sorex spp*). The *Sorex* group included two forest species that were difficult to distinguish in the field: the masked shrew (*S. cinereus*) and vagrant shrew (*S. vagrans*).

3.1. Effects of forest fragmentation

I captured sufficient numbers of red-backed voles, deer mice, and Uinta chipmunks in all sites to evaluate the effects of fragmentation on population density of these species. Red-backed voles demonstrated a negative response to all four measures of fragmentation, deer mice showed a positive response to all but edge density, and Uinta chipmunks had no apparent response (Table 4.2).

Capture rates of red-backed voles declined with an increase in the percentage of open areas, but capture rates among trap lines were highly variable, especially for low to moderately fragmented sites, and the Poisson regression explained 26% of the variance. For a graphical representation of the correlation, I plotted forest trap lines only (Fig. 4.2a), which accounted for 97% of the trap lines where voles were captured. I did not plot combined captures rates for forests and clearcuts since differences in capture rates between habitats were significant (see next section), resulting in different slopes for forest and clearcut capture rates.

Table 4.2. Statistical significance of habitat (mature forest versus clearcut) and fragmentation on capture rates of three species of small mammals, based on Poisson regressions.

Model: Captures/100 trap nights = *f* (habitat + percent of site unforested)

Species	P-value of habitat	P-value of % of site unforested	Model deviance	Total deviance	R^2
Red-backed vole	<0.001	0.031	179.24	693.30	0.26
Deer mouse	<0.001	0.013	267.75	729.61	0.37
Uinta chipmunk	0.709	0.114	4.31	200.74	0.02

Model: Captures/100 trap nights = *f* (habitat + percent of site in forest interior)

Species	P-value of habitat	P-value of forest interior	Model deviance	Total deviance	R^2
Red-backed vole	<0.001	0.012	186.84	693.30	0.27
Deer mouse	<0.001	<0.049	259.95	729.61	0.36
Uinta chipmunk	0.578	0.081	5.21	200.74	0.03

Model: Captures/100 trap nights = *f* (habitat + mean proximity index)

Species	P-value of habitat	P-value of mean proximity index	Model deviance	Total deviance	R^2
Red-backed vole	<0.001	0.008	196.99	693.30	0.28
Deer mouse	<0.001	<0.001	27.57	729.61	0.39
Uinta chipmunk	0.709	0.174	3.39	200.74	0.17

Model: Captures/100 trap nights = *f* (habitat + edge density)

Species	P-value of habitat	P-value of edge density	Model deviance	Total deviance	R^2
Red-backed vole	<0.001	0.004	196.33	693.30	0.28
Deer mouse	<0.001	0.190	252.04	729.61	0.35
Uinta chipmunk	0.575	0.079	5.24	200.74	0.03

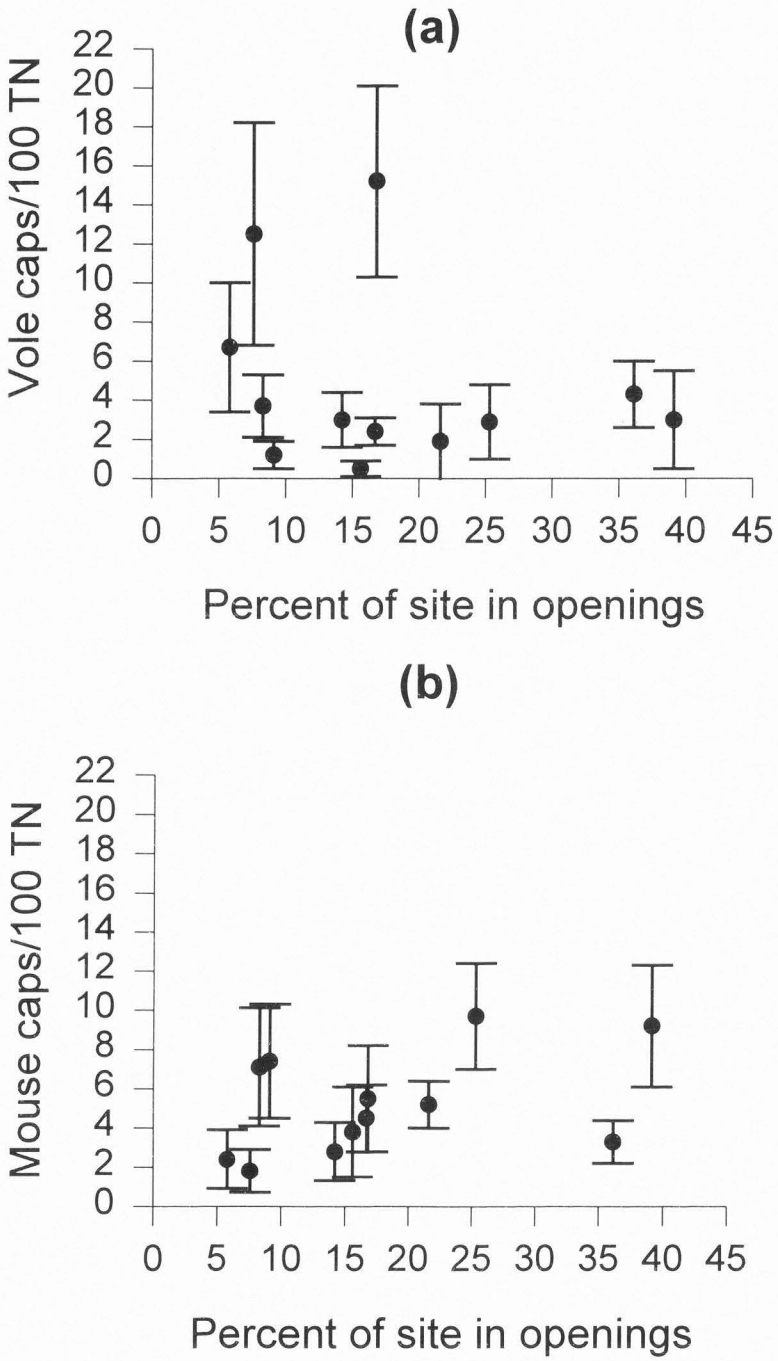


Fig. 4.2. Correlation of a) red-backed voles captures/100 trap nights and b) deer mouse captures/100 trap nights with increasing representation of open areas, showing means and 95% confidence intervals derived from 12 trap lines per site.

On forest trap lines, vole capture rates were highest in a site with 17% open areas (10% clearcuts, 7% natural openings, Fig. 4.1b), and second highest in a site with 8% of the landscape in natural openings and no clearcuts (Fig. 4.1a). The confidence intervals around mean capture rates for these sites were large due to extremely high vole captures on three trap lines. To test whether these extreme values were responsible for the overall correlation between vole captures and fragmentation, I removed these three trap lines from the analysis, but the association between capture rates and fragmentation remained significant ($\chi^2 = 4.62$, df = 1, $p = 0.03$, $R^2 = 0.27$).

Vole capture rates declined with reductions in forest interior habitat (Table 4.2), and the graphed relationship, not illustrated, was similar to that of open areas (Fig. 4.2a). Vole numbers decreased with an increase in proximity of open areas, as measured by the mean proximity index (Table 4.2, Fig. 4.3a). Vole capture rates were also negatively correlated with increase in edge density (Table 4.2, Fig. 4.4a).

Deer mouse capture rates increased with an increase in the percent of open areas, and the model explained 37% of the variance (Table 4.2). For a graphical comparison with vole captures, I plotted mouse capture rates for forest trap lines only (Fig. 4.2b). Deer mouse numbers increased in landscapes with less forest interior and shorter distances between open areas (mean proximity index). I observed no response to edge density with this species (Table 4.2, Fig. 4.4b).

Captures of Uinta chipmunks were not significantly correlated with any of the fragmentation measures (Table 4.2). I also did not observe a significant relationship between overall capture rates of small mammals and habitat fragmentation.

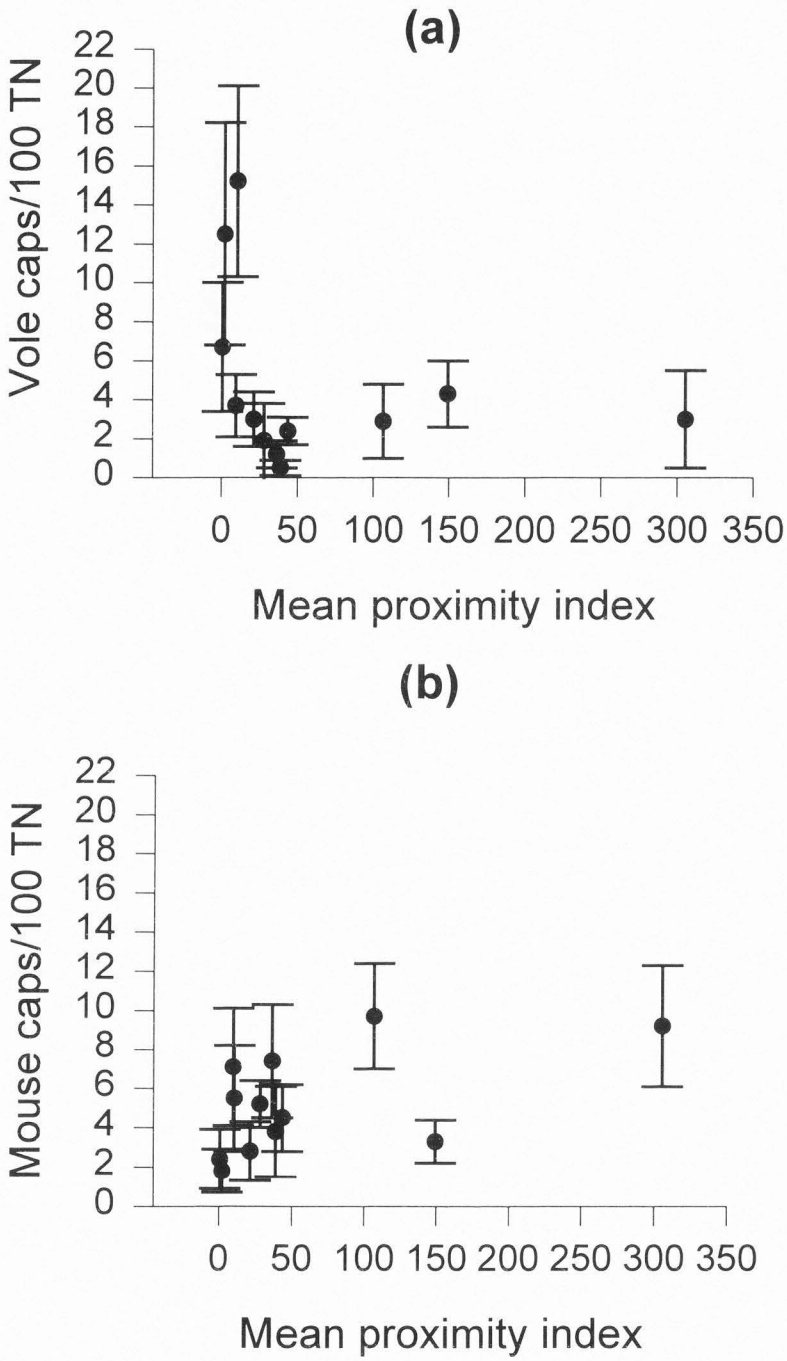


Fig. 4.3. Correlation of a) red-backed vole captures/100 trap nights and b) deer mouse captures/100 trap nights with increasing proximity of open areas, showing means and 95% confidence intervals derived from 12 trap lines per site.

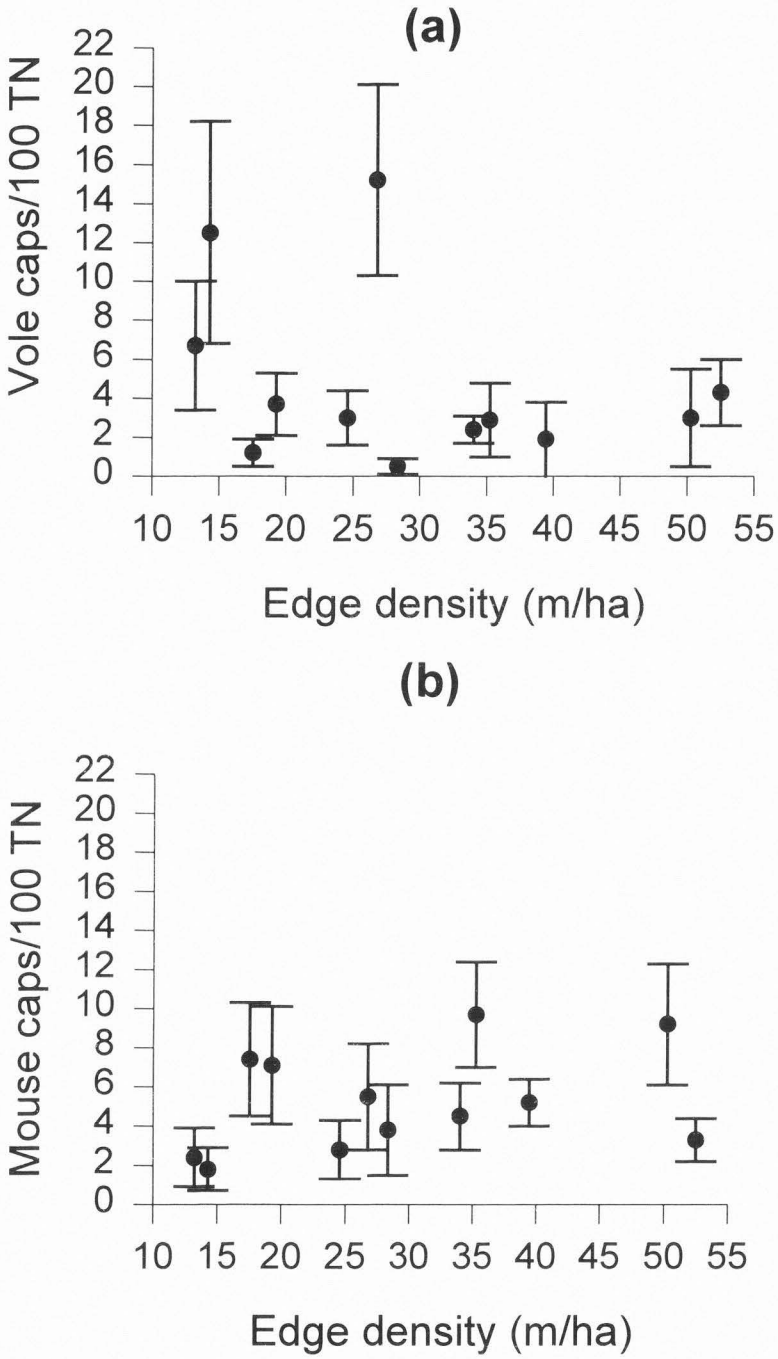


Fig. 4.4. Correlation of a) red-backed vole captures/100 trap nights and b) deer mouse captures/100 trap nights with edge density, showing means and 95% confidence intervals derived from 12 trap lines per site.

I observed no difference in species diversity with increasing fragmentation, as measured either with the Shannon-Weaver or Simpson's diversity indices. I captured 4-8 species per site, but species richness did not vary with fragmentation, e.g., the least and most fragmented sites yielded seven and nine species respectively. Detection of uncommon species was sporadic across all sites, and did not appear to be associated with the prevalence of open areas. Evenness also did not vary with fragmentation, because decreasing capture rates of red-backed voles were offset by increasing captures of deer mice (Fig. 4.2), and these species were the most prevalent in trap line samples.

3.2. Effects of habitat differences

Overall capture rates were highest in clearcuts and lowest in meadows, with significant differences among all three habitats (Table 4.3) (clearcuts versus forest, $\chi^2 = 18.15$, df = 1, $P < 0.001$; clearcuts versus meadows, $\chi^2 = 21.87$, df = 1, $p < 0.001$; forest versus meadows, $\chi^2 = 9.05$, df = 1, $p = 0.003$), although model fit was poor ($R^2 = 0.20$). Average biomass of captures per trap line, excluding snowshoe hare (*Lepus americanus*) was also highest in clearcuts, followed by forests and meadows (clearcuts versus forest, $T = -4.26$, $p < 0.001$; clearcuts versus meadows, $T = 5.55$, $p < 0.001$; forest versus meadows, $T = 4.66$, $p < 0.001$). Species diversity differed among habitats, with the highest diversity in forests and lowest in meadows, as measured by both indices (Table 4.3) (Shannon-Weaver, $F = 2.83$, df = 1, $p = 0.09$; Simpson's D, $F = 2.45$, df = 1, $p = 0.06$).

Individual species comparisons between habitats were restricted to trap lines in

Table 4.3. Summary of small-mammal community measures in three habitats within the Uinta Mountains of northern Utah.

	Forest (N = 89)		Clearcuts (N = 36)		Meadows (N = 9)	
	Mean	SD	Mean	SD	Mean	SD
Captures/100 trap nights	13.8	7.5	21.2	11.4	6.4	9.8
Trap line biomass (g)[1]	285.0	164.0	420.0	244.0	106.0	132.0
Shannon-Weaver H	0.9	0.4	0.7	0.4	0.5	0.4
Simpson's D	2.3	0.8	1.9	0.8	1.8	0.6

[1] excluding hares

forests (n = 89) and clearcuts (n = 36), because of the low number of trap lines (n = 9) and low capture rates in meadows. Red-backed voles were trapped at significantly higher rates in forests than in clearcuts (χ^2 = 16.7, df = 1, p = < 0.01), whereas deer mice (χ^2 = 56.03, df = 1, p < 0.01) and least chipmunks (χ^2 = 52.31, df = 1, p < 0.01) were more frequently trapped in clearcuts. Uinta chipmunks were equally abundant in both habitats. I found masked/vagrant shrews in both habitats, but capture rates were higher in forests (χ^2 = 3.41, df = 1, p = 0.07) (Table 4.2).

The large number of deer mice caught in both clearcuts and forests enabled me to examine the relationship between habitat and age class distribution. Using a mixed model analysis with site as a blocking factor, I compared the proportion of adults found in clearcuts and forests within 10 sites where clearcuts were present, and found no difference in age class distribution between habitats (site F = 1.62, df = 9, P = 0.24; habitat F = 0.06, df = 1, P = 0.80; site x habitat F = 1.27, df = 9, P = 0.26). In forests, 64% of trapped deer mice were adults, compared to 55% in clearcuts.

4. Discussion

Habitat fragmentation from the combined effects of natural openings and clearcut blocks appeared to affect densities of southern red-backed voles and deer mice, based on the correlations observed between capture rates and four measures of fragmentation. Both species responded to loss and gain in habitat area, measured by the shift in proportional representation of forest and open areas, with lower densities of red-backed voles densities and higher densities of deer mice in landscapes with greater proportions of open areas. In all cases, the strength of the relationship between capture rates and fragmentation was not strong, because I did not differentiate between traps placed in habitat interior or near edges, and animals whose home ranges were distant from clearcuts were included in the overall capture rate per trap line. Given this lack of distinction, the observed response is noteworthy.

To examine whether the apparent effects of landscape pattern were additive to habitat loss, I generated a null model predicting a reduction in voles from habitat loss only, and compared the predicted values with my data (Fig. 4.5). The null model was developed by using the mean capture rate from the three least-fragmented sites to project a base level capture rate in unfragmented habitat, and setting all other capture rates as a fraction of the base level, proportional to the amount of habitat lost. Capture data from the remaining sites were significantly lower than expected from loss of habitat alone (T = 3.14, P = 0.02), supporting the interpretation that the combined effects of habitat loss and landscape pattern were responsible for the observed decline in capture rates.

A key aspect of landscape pattern is the amount of forest interior habitat. During the process of fragmentation, forest interior disappears at a faster rate than total forest

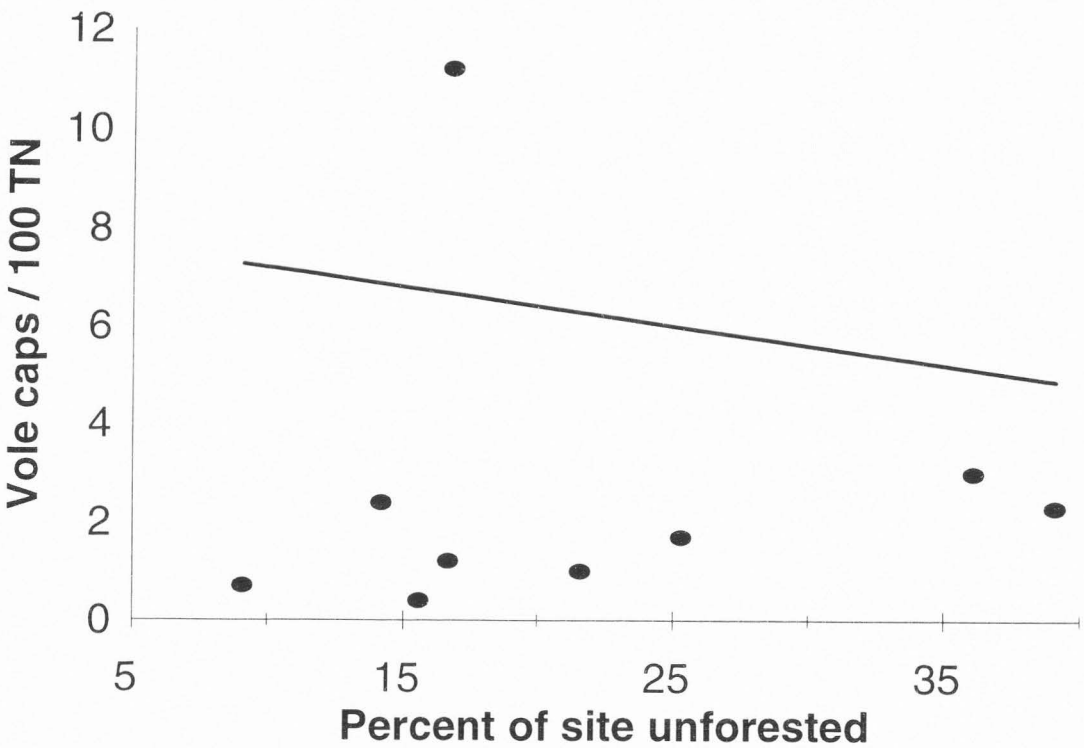


Fig. 4.5. Observed capture rates of red-backed voles (circles) compared to expected decline in vole capture rates based on proportional loss of forest habitat (solid line).

habitat because narrow strips of forest between open areas lack forest interior. In this study, the most fragmented site was 61% forested, but only 36% was in forest interior. The rate of decline in red-backed vole captures appeared to echo the loss of forest interior more closely than loss of total forest habitat.

For red-backed voles, loss of forest interior and increase in forest edge may be detrimental due to changes in temperature and moisture conditions near forest edges (Waring and Schlesinger 1985). In Oregon, Mills (1995) captured fewer California red-backed voles in small remnants of forest than in larger blocks, and he also found preliminary evidence that forest edge microclimates were less suitable for hypogeous sporocarps of mycorrhizal fungi, the primary food item for California red-backed voles. Although the relationship between southern red-backed voles and food supply in edge habitat has not been investigated to the same degree as California red-backed voles, there is evidence that this species may also be sensitive to edge conditions. In British Columbia, significantly fewer southern red-backed voles were captured within 35 m of clearcuts than in forest interiors (Walters 1991). Edge conditions can extend > 50 m into the forest (Lovejoy *et al.* 1986), and in the most fragmented site in my study (Fig. 4.1d), mean nearest neighbor distances between openings was 75 m. Thus, much of the forest habitat found between clearcuts in highly fragmented landscapes had microclimatic conditions of edge habitat.

Variation in capture rates of voles was high when open areas occupied < 20 % of the landscape, implying less sensitivity to landscape pattern when fragmentation was sufficiently low for most forest area to contain interior habitat (Fig. 4.1a, b, Fig. 4.2). A

noticeable reduction in the variance of vole captures was observed when open areas surpassed 20% of the total area, and the proximity of these openings caused forest interior to occupy half of the landscape or less (Figs. 4.1c, 4.1d, and 4.3). At this point, landscape pattern appeared to be limiting to vole populations.

In contrast, the juxtaposition of open areas with forest appeared to favor deer mice. The increase in capture rates of mice roughly corresponded to the fragmentation level that elicited a negative response from voles (Fig. 4.2), although this does not imply competitive interactions between the species. The increase in deer mice in forests may be due to dispersal from adjacent clearcuts, where densities were higher.

Walters (1991) proposed that clearcuts may act as sink habitat for deer mice, as he found significantly greater proportions of juvenile to adult females in burned clearcuts. My data do not support this proposal. Although juvenile ratios were somewhat higher in clearcuts than in forests, the difference in juvenile representation between the two habitats was not significant.

At the scale of habitat comparisons, my findings supported previously reported differences in the composition of small-mammal communities between clearcuts and forests (Gashwiler 1970). Although capture rates were highest in clearcuts, species richness was highest in forests. Capture rates in meadows were substantially lower than other habitats.

Infrequent captures of montane voles (*Microtus montanus*) in meadows suggest a possible low point in the population cycle of this species during the survey period. In addition, approximately half of the meadow sites contained domestic livestock during or

immediately prior to the surveys, which reduced plant biomass and increased trap disturbance, potentially affecting small-mammal populations and capture rates of meadow species.

In summary, clearcut harvest methods appeared to alter small-mammal populations at the 9-km^2 landscape scale as well as individual cut block scale. Clearcut timber harvests affected small-mammal community composition in the short term through abrupt changes in vegetation and habitat structure. Multiple cut blocks altered landscape pattern and increased the amount of forest edge, resulting in more xeric microsite conditions for red-backed voles and greater habitat opportunities for deer mice. The duration of these effects at both scales is expected to vary with the rate of seral advancement of the forest cover type.

The influence of fragmentation on small-mammal populations can ultimately affect populations of larger species that consume small mammals. For example, fragmentation patterns that favor deer mice over red-backed voles may cause reductions in American marten (Hargis and Bissonette, unpubl. data), because this species preys more heavily on red-backed voles than deer mice (Martin 1994).

Timber harvest patterns that result in aggregated rather than dispersed cut blocks can reduce potential impacts to voles and other forest species by retaining larger areas of forest interior (Franklin and Forman 1987). I support this approach, because both edge and interior species can benefit. When cut blocks are aggregated, the amount of edge is the same as under dispersed cutting for similar-size cut blocks, and the resulting open areas are in greater proximity, thus favoring species with small home ranges that thrive in

landscapes with close juxtaposition of different patch types. At the same time, the interior value of larger forest patches is maintained. The location and prevalence of natural openings should be factored into the aggregated cutting pattern of each landscape, because they represent a baseline of natural fragmentation that must be included in the total design.

References

Edwards, T.C. Jr., Homer, C.G., Bassett, S.D., Falconer, A., Ramsey, R.D. and Wight, D.W. 1995. Utah gap analysis: an environmental information system. Utah Coop. Fish and Wildlife Research Unit, Technical Report 91-1.

Franklin, J.F. and Forman, R.T.T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landsc. Ecol. 1: 5-18.

Frome, E.L., Kutner, M.H. and Beauchamp, J.J. 1973. Regression analysis of Poisson-distributed data. J. Am. Stat. Assoc. 68: 935-940.

Gashwiler, J.S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecol. 51: 1018-1026.

Gunther, P.M., Horn, B.S. and Babb, G.D. 1983. Small-mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Sci. 57: 32-44.

Gustafson, E.J. and G.R. Parker. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. Landsc. Ecol. 7: 101-110.

Kendall, M.G. and Stuart, A. 1946. The advanced theory of statistics, vol. 2. Hafner

Publishing Co., New York.

Kleinbaum, D.G., Kupper, L.L. and Muller K.E. 1988. Applied regression analysis and other multivariable methods. PWS-KENT Publ. Co., Boston, Mass.

Lovejoy, T.E., Bierregaard, R.O. Jr., Rylands, A.B., Malcom, J.R., Quintela, C.E., Harper, L.H., Brown, K.S. Jr., Powell, A. H., Powell, G.V.N., Schubart, H.O.R. and Hays, M.B. 1986. Edge and other effects of isolation on Amazon forest fragments. *In* Conservation biology: the science of scarcity and diversity. pp. 257-285. Edited by M.E. Soulé. Sinauer Associates, Sunderland, Massachusetts.

Martin, S. K. 1994. Feeding ecology of American martens and fishers. *In* Martens, sables, and fishers: biology and conservation. pp. 297-315. Edited by S.W. Buskirk, A.S. Harestad, M.G. Raphael and R. A. Powell. Cornell Univ. Press, Ithaca, New York.

McCullagh, P. and Nelder, J. A. 1991. Generalized linear models. Chapman and Hall, New York.

McGarigal, K. and Marks, B.J. 1995. FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. U.S. Forest Service Gen. Tech. Report PNW-GTR-351.

Mills, L.S. 1995. Edge effects and isolation: red-backed voles on forest remnants. Cons. Biol. 9: 395-403.

Petticrew, B. G. and Sadleir, R.M.F.S. 1974. The ecology of the deer mouse *Peromyscus maniculatus* in a coastal coniferous forest. I. Populations dynamics. Can. J. Zool. 52: 107-118.

Ramirez, P. Jr. and Hornocker, M. 1981. Small mammal populations in different-aged clearcuts in northwestern Montana. J. Mammal. 62: 400-403.

SAS Institute, Inc. 1993. SAS/STAT software: The GENMOD procedure, release 6.09. SAS Technical Report P-243, SAS Institute, Cary, North Carolina.

Scrivner, J.H. and H.D. Smith. 1984. Relative abundance of small mammals in four successional stages of spruce-fir forest in Idaho. Northwest Sci. 58: 171-176.

Shannon, C.E. and Weaver, W. 1949. The mathematical theory of communication. Univ. Illinois Press, Urbana.

Simpson, E.H. 1949. Measurement of diversity. Nature 163: 688.

Walters, B.B. 1991. Small mammals in a subalpine old-growth forest and clearcuts. Northwest Sci. 65: 27-30.

Waring, R.H. and Schlesinger, W.H. 1985. Forest ecosystems: concepts and management. Academic Press, Inc., Orlando, Florida.

Whitcomb, R.F., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K. and Bystrak, D. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. *In* Forest island dynamics in man-dominated landscapes. pp. 125-205. Edited by R.L. Burgess and D.M. Sharpe. Springer-Verlag, New York.

CHAPTER 5

SYNTHESIS

Habitat fragmentation results in both loss of habitat and development of new landscape patterns. Most species will respond negatively to loss of habitat unless food availability or access to sites used for mating or rearing of young are not affected. However, responses to landscape pattern will be more variable because species respond to the size, shape, and spatial distribution of patches in different ways, and some landscape patterns are more detrimental for a given species than other patterns.

The American marten and a common prey, the red-backed vole, both appear to respond negatively not only to loss of habitat, but to landscape patterns that reduce the availability of forest interior. When patches of open areas are small, interior habitat is reduced more readily than in landscapes with the same amount of open areas in large patches. Also, small patches reduce interior habitat more quickly if they are widely dispersed rather than closely spaced.

The observed responses of martens and voles to spatial pattern are difficult to separate from loss of habitat using the study design I developed, because habitat loss and changes in landscape pattern occurred simultaneously. As demonstrated in Chapter 2, there is high correlation between loss of habitat and the values derived from several measures of landscape pattern.

Martens and voles may be sensitive to landscape pattern alone, when loss of habitat area is held constant. This hypothesis could be tested by surveying populations

within a series of landscapes with the same amount of habitat area but different landscape pattern. I predict that both species would occur in fewer numbers in landscapes where the pattern of patch dispersal caused the greatest reduction in forest interior habitat.

If these species are sensitive to landscape pattern alone, more work is also needed on the underlying mechanisms that illicit a negative response. As proposed in Chapter 3, marten response to loss of forest interior may be linked to reduced vole densities in edge habitat. This hypothesis can be tested by comparing vole capture rates in forest interior and in narrow strips of forest between clearcuts, with the prediction that capture rates between clearcuts would be lower. If this prediction were realized, the mechanisms causing fewer voles on forest edges could also be explored.

There is sufficient evidence that climatic conditions on forest edges differ from conditions in forest interior (Waring and Schlesinger 1985, Lovejoy et al. 1986, Chen et al. 1992), but more information is needed on the relationship between microclimatic factors and food resources for red-backed voles. Diets are known to include fungi, lichens, conifer seeds, berries, and occasional invertebrates (Gunther et al. 1983), and the availability of some food resources may differ with air or soil moisture, temperature, or wind speed.

The careful design of landscape pattern may play a significant role in modifying the effects of habitat fragmentation for many species. Where fragmentation is due to human activities, it may be possible to design landscapes that reduce the impacts from loss of habitat. In particular, this may mean aggregating the loss of habitat into a single, large patch rather than several small, dispersed patches, or in creating a single cluster of smaller

patches confined within one portion of the landscape. The latter design would result in the same edge availability as dispersed patches, thereby benefiting edge-associated species, but edge effects would be localized.

Ironically, legislation created to minimize wildlife impacts from timber harvests has resulted in landscape patterns that exacerbate rather than reduce the effects of habitat fragmentation. Upper bounds on clearcut patch size were set by 36 CFR Part 219 (U.S. Department of Agriculture 1982) under the National Forest Management Act of 1976, a legal action that has resulted in patterns of widely dispersed, small clearcuts in managed forests throughout the United States.

Changing the law may prove easier than changing the landscape patterns resulting from the law. Wallin et al. (1994) used landscape simulations to test the effects of different cutting patterns on landscape pattern over 300 years, and found that shifting a landscape pattern from many small patches to few, large patches was difficult to accomplish, unless no timber was harvested for a period of 50 years to allow regeneration of previously cut areas.

Differences in the spatial distribution of patches are not only difficult to change, but also difficult to quantify. In my investigations of edge density, contagion, mean nearest neighbor distance between patches, mean proximity index, perimeter-area fractal dimension, and mass fractal dimension, none of these measures was able to differentiate between landscapes with dispersed versus clumped patches.

This raises the question whether any landscape metric is able to distinguish the spatial distribution of patches, and suggests avenues for further research. Effective

measures would need to include a term that quantified the distance from a patch or clump of patches to the boundary of the landscape, a term that is lacking in all metrics I examined. Apparently this issue has not been adequately addressed to date, because much of the published literature erroneously assumes that certain measures are sensitive to spatial distribution. The results of my study may be the first evidence to the contrary.

For example, Li and Reynolds (1993) assumed that their modified version of the contagion index (O'Neill et al. 1988) was able to differentiate aggregated versus random or uniform distribution of patches. However, because aggregations allowed patch size to increase, larger contagion values were due to increased patch area rather than the aggregated distribution of patches. McGarigal and Marks (1994) also assumed that contagion was sensitive to spatial distribution in their description of this measure for users of the FRAGSTATS spatial pattern analysis program.

Lacunarity, a measure of landscape texture based on the variance in fractal measurements over increasing spatial subsamples, is also believed to measure patterns of spatial dispersion (Plotnick et al. 1993), but this is only an assumption made by the authors with no evidence of validation. My investigations of mass fractal dimension, a measure from which lacunarity can be derived, indicated no sensitivity to spatial distribution. Lacunarity provides information on the range of patch sizes contained within a landscape, but does not measure how the patches are spatially dispersed.

Papers comparing landscape patterns often use the term "aggregation" to mean a spatially clumped patch distribution and assume that they are quantifying this distribution when in fact they are quantifying aggregation of a class into larger patch sizes. Li et al.

(1993) used edge density, area-weighted shape, habitat patchiness, and an interior area fragmentation index to compare aggregated versus dispersed cutting patterns, but none of these measures is sensitive to spatial distribution. They simply quantify differences due to larger patch sizes used in aggregated cutting design.

Ripple et al. (1991) have proposed a measure coined GISFrag that is presumably able to differentiate spatial distributions of patches, but I did not include this measure in my analysis, and the authors do not demonstrate this capability with landscapes that have different spatial distributions. There may exist several measures that are sensitive to the spatial distribution of patches, but conducting a complete search was beyond the scope of my study. Nevertheless, I can report that the inability to detect spatial distribution was a limitation in all measures I examined, and may suggest an area for the future advancement of spatial measures.

LITERATURE CITED

Chen, J., J. F. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth douglas-fir forests. Ecological Applications **2**:387-396.

Gunther, P. M., B. S. Horn, and G. D. Babb. 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Science **57**:32-44.

Li, H., J. F. Franklin, F. J. Swanson, and T. A. Spies. 1993. Developing alternative forest cutting patterns: a simulation approach. Landscape ecology **8**:63-75.

Li, H., and J. F. Reynolds. 1993. A new contagion index to quantify spatial patterns of landscapes. Landscape Ecology **8**:155-162.

Lovejoy, T. E., R. O. Bierregaard, Jr., A. B. Rylands, J. R. Malcom, C. E. Quintela, L. H. Harper, K. S. Brown, Jr., A. H. Powell, G. V. N. Powell, H. O. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 *in* M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts, USA.

McGarigal, K., and B. J. Marks. 1994. FRAGSTATS spatial analysis program for quantifying landscape structure. Forest Science Department, Oregon State University, Corvallis, Oregon, USA.

O'Neill, R. V., J. R. Krummel, R. H. Gardner, G. Sugihara, B. Jackson, D. L. DeAngelis, B. T. Milne, M. G. Turner, B. Zygmunt, S. W. Christensen, V. H. Dale, and Graham, R. L. 1988. Indices of landscape pattern. Landscape Ecology **1**:153-162.

Plotnick, R. E., R. H. Gardner, and R. V. O'Neill. 1993. Lacunarity indices as measures of landscape texture. Landscape Ecology **8**:201-211.

Ripple, W. J., G. A. Bradshaw, and T. A. Spies. 1991. Measuring forest landscape patterns in the Cascade Range of Oregon, USA. Biological Conservation **57**:73-88.

U. S. Department of Agriculture. 1982. National Forest System land and resource management planning. 36 CFR Part 219. Federal Register **47**:43051.

Wallin, D. O., F. J. Swanson, and B. Marks. 1994. Landscape pattern response to

changes in pattern generation rules: land-use legacies in forestry. Ecological Applications **4**:569-580.

Waring, R. H., and W. H. Schlesinger. 1985. Forest ecosystems: concepts and management. Academic Press, Inc., Orlando, Florida, USA.

APPENDIX. LETTERS OF RELEASE FROM COAUTHORS

August 9, 1996

Dr. Christina D. Hargis
Dept. of Fisheries and Wildlife
Utah State University
Logan, UT 84322

Dear Dr. Hargis,

As coauthor, I give my permission for you to include the following material in your dissertation:

Chapter 2:
The Behavior of Landscape Metrics Commonly Used in the Study of Habitat Fragmentation.

Sincerely,

John L. David

August 9, 1996

Dr. Christina D. Hargis
Dept. of Fisheries and Wildlife
Utah State University
Logan, UT 84322

Dear Dr. Hargis,

As coauthor, I give my permission for you to include the following material in your dissertation:

Chapter 3:
The Influence of Forest Fragmentation on American Marten Populations.

Sincerely,

David L. Turner

CURRICULUM VITAE

CHRISTINA D. HARGIS

Utah State University
Department of Fisheries and Wildlife
Logan, UT 84322-5210
Home office phone: (801) 753-5607

OVERVIEW

My career interests and qualifications are in wildlife habitat management and applied wildlife research. I specialize in forested ecosystems, but have also worked in western shrub and grassland communities. My research has focused on wildlife responses to habitat factors at a variety of spatial scales. I have expertise in landscape ecology, particularly the quantification of landscape patterns and the influence of these patterns on carnivores and small mammals. I recently completed my doctorate in Wildlife at Utah State University, and my doctoral research investigated the effects of forest fragmentation on the American marten. I have an M.S. in wildland resource science, and 10 years of experience as a wildlife biologist with the Forest Service. My combined research and management experience provide an excellent background for employment in applied wildlife research.

EDUCATION

Ph.D. Wildlife, Utah State University, Logan, Utah. 1996. Dissertation: The influence of forest fragmentation and landscape pattern on American martens and their prey.

M.S. Wildland Resource Science, University of California, Berkeley. 1981. Thesis: Winter habitat use and food habits of pine marten in Yosemite National Park.

B.A. Chinese Language and Literature, University of Washington, Seattle. 1971.

TEACHING AND PRESENTATION EXPERIENCE

Invited instructor for Region 3 Forest Service training in ecosystem management. Three sessions: Prescott, AZ in March, 1995; Albuquerque, NM, in April, 1995; and Phoenix, AZ in November, 1995. Topic: Developing a monitoring framework for ecosystem management.

Invited lecturer, graduate level course in landscape ecology at Utah State University, October, 1994. Topic: Chaos theory.

Invited lecturer, upper division course in wildlife management, Utah State University, May, 1993. Topic: Integrating silvicultural objectives with wildlife habitat management.

Invited speaker, U. C. Berkeley Wildlife Dept. Seminar, Oct, 1985. Topic: Interagency cooperation and the reintroduction of Sierra Nevada mountain sheep.

Natural history interpreter for the National Park Service for five summer seasons, 1976-1980. Presented 1-hour programs with and without the aid of audio-visual equipment.

Environmental education instructor, National Park Service, summer 1975. Designed curriculum for the Junior Ranger Program and instructed weekly sessions.

Environmental education instructor, Yosemite Institute, academic year 1973-74. Junior high and high school field classes in ecology.

PRESENTATIONS

Hargis, C. D., J. A. Bissonette, and J. L. David. The behavior of fragmentation measures when landscapes move from random to real. Second National Conference, The Wildlife Society, Portland, OR. September, 1995.

Hargis, C. D., and J. A. Bissonette. The effects of forest fragmentation on American marten and their prey. Second International Symposium on Martens and Fishers, Edmonton, Alberta. August, 1995.

Hargis, C. D., C. McCarthy, and R. D. Perloff. Home ranges and habitats of northern goshawks in eastern California. Annual meeting of the Cooper's Ornithological Union, Sacramento, CA. April, 1993.

Hargis, C. D., and J. A. Bissonette. The use of fractal dimension in differentiating landscape pattern. Annual meeting of the Utah Chapter of The Wildlife Society, St. George, UT. March, 1993.

Hargis, C. D. and C. McCarthy. Vegetation changes following a prescribed burn on a Great Basin meadow. Annual meeting of the Western Section of The Wildlife Society. Reno, NV 1983.

PUBLICATIONS

Hargis, C. D., C. McCarthy, and R. D. Perloff. 1994. Home ranges and habitats of northern goshawks in eastern California. Studies in Avian Biology 16:66-74.

Bleich, V. C., C. D. Hargis, J. A. Keay, and J. D. Wehausen. 1991. Interagency coordination and the restoration of wildlife populations. Pp. 277-284 *in* J. Edelbrock and S. Carpenter, eds. Natural areas and Yosemite: Prospects for the future. USDI National Park Service, Denver Service Center, Denver, CO.

Hargis, C. D. and C. McCarthy. 1986. Vegetation changes following a prescribed burn on a Great Basin meadow. Trans. West. Sec. Wildl. Soc. 22:47-51.

McCarthy, C. and C. Hargis. 1984. Analyzing wildlife habitat at the project level:an evaluation method. Trans. West. Sec. the Wildl. Soc. 20:73-80.

Hargis, C. D., J. D. Wehausen, D. Graber and J. Keay. 1984. Sierra Nevada bighorn sheep recovery and conservation plan. Inyo N.F. 16pp.

Hargis, C. D. and D. R. McCullough. 1984. Winter diet and habitat selection of marten in Yosemite National Park. J. Wildl. Manage. 48:140-146.

Hargis, C. D. 1982. Winter habitat utilization and food habits of pine martens in Yosemite National Park. Coop. Nat. Park Res. Studies Unit, Tech. Rep. No. 6. 59pp.

SUBMITTED MANUSCRIPTS

Hargis, C. D., John A. Bissonette, and John L. David. The behavior of landscape metrics commonly used in the study of habitat fragmentation (Submitted to Landscape Ecology.)

Hargis, C. D., John A. Bissonette, and David L. Turner. The influence of forest fragmentation and landscape pattern on American martens. (Submitted to Ecological Applications.)

Hargis, C. D., and John A. Bissonette. The effect of forest fragmentation on American marten populations and prey availability. (Proceedings for the Second Annual Symposium on Marten and Fisher.)

Hargis, C. D., and John A. Bissonette. Landscape-level effects of timber harvests on small mammal populations in spruce-fir forests (In prep for Journal of Wildlife Management.)

Hargis, C. D., John A. Bissonette, and John L. David. Understanding measures of landscape pattern. (Accepted as a chapter in A Primer in Landscape Ecology, to be published by Springer-Verlag.)

WORK EXPERIENCE

Wildlife biologist (GS 486-11) Supervisor: Dave Turner
Duration: February 1994-October 1995 (801)755-3560
Coop Ed/intermittent pay status

Statistical Aspects of Monitoring
Forestry Sciences Lab, Logan, UT 85341

This position was designed to provide training for an eventual placement as research wildlife biologist with the Forest Service Intermountain Research Station. The work was intermittent to allow time for doctoral research. I provided technical assistance to the Bitterroot National Forest in developing a framework for monitoring ecosystem health. I also was detailed as an instructor for regional-level ecosystem management training for Forest Service employees in Arizona and New Mexico.

Research Assistant Supervisor: John Bissonette
Duration: October, 1990 to present (801)797-2511

Dept. of Fisheries and Wildlife
Utah State University, Logan, UT 84322-5210

As a Ph.D. candidate in wildlife, I conducted a landscape-level study on the influence of forest fragmentation on American marten and their prey. This involved three years of field research and an additional year of GIS analysis.

Through dissertation research, I have developed expertise in applied landscape ecology, particularly the quantification of landscape patterns and the influence of these patterns on marten and small mammals. I am well-versed in current literature pertaining to landscape ecology theory and application, and continue to stay current through regular communications with other ecologists in this field.

I have gained proficiency in numerous computer applications developed for DOS, Microsoft Windows, Macintosh, and Unix operating systems, including geographical information systems, statistical packages, spreadsheets, graphics, and bibliographic reference programs.

Wildlife biologist (GS 486-11) Supervisor: Bill Bramlette
Duration: 1987-1990 (619)873-2400

Mono Lake Ranger District, Lee Vining, CA 93541

I was responsible for the wildlife program on two ranger districts and:
- Administered a $100,000 annual budget
- Supervised a GS-7 bio-tech and 1-3 summer employees
- Planned and implemented wildlife habitat improvement projects, including bitterbrush planting, snag protection, road closures, prescribed burns, and water developments
- Provided written input to resource planning documents such as timber sales, proposed geothermal developments, and proposed ski areas
- Served as chairperson of the Sierra Nevada Mountain Sheep Interagency Advisory Group.

In addition, I was involved in the following special projects:
- Designed and conducted a 3-year radio telemetry study of goshawk home range and habitat use
- Designed and conducted a study on the "life expectancy" of snags under various management practices
- Served as an interdisciplinary team member for preparation of the Mono Basin National Forest Scenic Area Comprehensive Management Plan and EIS
- Served as the Mono Basin National Forest Scenic Area Manager for 4 months during extended leave of the incumbent.

Wildlife biologist (GS 486-9) Supervisor: Clint McCarthy
Duration: 1981-1987 (406)657-6361

I was responsible for the wildlife program on the Mono Lake Ranger District and:
- Administered a $60,000 annual budget
- Supervised 1-3 summer temporary employees
- Planned and implemented wildlife habitat improvement projects
- Served as a member of the Sierra Nevada Mountain Sheep Interagency Advisory Group and was an author of the Recovery Plan prepared by this group
- Assisted in development of a habitat survey technique for providing quantitative wildlife input to timber sales.

In addition, I was involved in the following special projects:
- Served as project leader for a mountain sheep reintroduction, including writing the environmental assessment, assisting with the capture and relocation effort, and working cooperatively with Yosemite National Park (the summer range) and U.C. Berkeley (Dr. Reg Barrett) to establish a 3-year monitoring study of the new herd.
- Worked cooperatively with BLM and U.C. Berkeley (Dale McCullough) to set up a monitoring study of a pronghorn reintroduction
- Designed and implemented a 5-year monitoring study of vegetation changes following a prescribed burn in rangeland.

Research Assistant — Supervisor: Reg Barrett
Duration: 1978-1980 — (510)642-7261

I was field supervisor for a rare carnivore survey conducted by Dr. Reg Barrett. I surveyed each square km of a 100 km^2 study area, using hair snares and sooted track plots. I also collected habitat data, conducted microscopic analysis of hairs found in snares, and supervised one field employee.

I assisted Ph.D. candidate David Graber with a bear ecology study in Yosemite National Park. I completed a diet analysis based on 400 bear scat samples and collected field observations on bear behavior. I also assisted with sedation and data collection of black bears.

Biological Technician (GS 5) — Supervisor:Jim Brady
Duration: 1974-1977

I worked as a backcountry ranger in Yosemite Park. In the winter, I was a winter patrol ranger and logged approximately 800 nordic ski miles each winter during patrol duty. I also assisted with snow surveys for the California Dept. of Water Resources.

In the summer, I was assigned to a heavily-used backpacking area which had a frequency of human/black bear encounters. My duties were to educate backpackers in proper behavior around bears and in the appropriate ways to secure food. I also intervened in numerous bear encounters which could have resulted in food loss, damage to equipment, or human injury. I also recorded bear movements and behavior for the park biologist.

HONORS, AWARDS, AND FELLOWSHIPS

Full-tuition scholarship, University of Washington, Seattle, 1967-68.

Forest Service Certificates of Merit, 1984 and 1985

Forest Service Quality Step Increase for superior performance, 1986

President's Fellowship ($7,000), Utah State University, 1990

REFERENCES

Dr. John A. Bissonette. (801) 797-2511. Leader, Utah Cooperative Fish and Wildlife Research Unit (NBS)at Utah State Univerity, Logan, Utah.

Dr. Ray Dueser. (801) 797-2459. Department Head, Department of Fisheries and Wildlife, Utah State University, Logan, UT.

Dr. Michael Conover. (801) 797-2436. Professor, Fisheries and Wildlife, Utah State University, Logan, UT.

Journal of Applied Ecology 1999, **36**, 157–172

The influence of forest fragmentation and landscape pattern on American martens

CHRISTINA D. HARGIS, JOHN A. BISSONETTE* and DAVID L. TURNER†

*USDA Forest Service, South-west Forest Science Complex, 2500 S. Pine Knoll, Flagstaff, AZ 86001, USA; *Utah Cooperative Fish and Wildlife Research Unit (USGS-BRD), Department of Fisheries and Wildlife, Utah State University, Logan, UT 84322–5290, USA; and †USDA Forest Service Intermountain Research Station, 860 N 1200 E, Logan, UT 84321, USA*

Summary

1. We investigated the effects of forest fragmentation on American martens (*Martes americana* Rhoads) by evaluating differences in marten capture rates (excluding recaptures) in 18 study sites with different levels of fragmentation resulting from timber harvest clearcuts and natural openings. We focused on low levels of fragmentation, where forest connectivity was maintained and non-forest cover ranged from 2% to 42%.

2. Martens appeared to respond negatively to low levels of habitat fragmentation, based on the significant decrease in capture rates within the series of increasingly fragmented landscapes. Martens were nearly absent from landscapes having > 25% non-forest cover, even though forest connectivity was still present.

3. Marten capture rates were negatively correlated with increasing proximity of open areas and increasing extent of high-contrast edges. Forested landscapes appeared unsuitable for martens when the average nearest-neighbour distance between open (non-forested) patches was < 100 m. In these landscapes, the proximity of open areas created strips of forest edge and eliminated nearly all forest interior.

4. Small mammal densities were significantly higher in clearcuts than in forests, but marten captures were not correlated with prey abundance or biomass associated with clearcuts.

5. Conservation efforts for the marten must consider not only the structural aspects of mature forests, but the landscape pattern in which the forest occurs. We recommend that the combination of timber harvests and natural openings comprise <25% of landscapes $\geqslant 9\,km^2$ in size.

6. The spatial pattern of open areas is important as well, because small, dispersed openings result in less forest interior habitat than one large opening at the same percentage of fragmentation. Progressive cutting from a single patch would retain the largest amount of interior forest habitat.

Key-words: edge density, habitat fragmentation, *Martes americana*, proximity index, timber harvests.

Journal of Applied Ecology (1999) **36**, 157–172

Introduction

The modification of forested landscapes through land management practices has fostered a growing interest in the effects of habitat fragmentation on wildlife. Habitat fragmentation, originally defined as the formation of isolated fragments from a formerly continuous habitat (Wilcox 1980; Harris 1984), has taken on a broader meaning in recent times, reflecting an awareness that fragmentation can affect organisms long before the original habitat is reduced to remnant patches. In the fullest sense, fragmentation is disruption in continuity in any temporal or functional

Correspondence: Christina D. Hargis (fax: (520) 556 2131; e-mail: cdh@alpine.for.nau.edu).

domain (Lord & Norton 1990). Habitat fragmentation occurs along a continuum, from landscapes dominated by the original cover type to landscapes where the original type is reduced to remnant patches.

The majority of habitat fragmentation studies have focused on extreme examples of fragmentation, after the original cover type has ceased to function as the dominant landscape element. By focusing on remnant habitat patches, these studies have examined the effect that patch area and isolation have on population size, extinction and recolonization rates, and dispersal rates of individual species, as well as on species diversity (Diamond 1975; Whitcomb *et al.* 1981; Harris 1984; Rosenberg & Raphael 1986; Verboom & van Apeldoorn 1990). More recently, investigations have turned to less extreme cases of fragmentation, and have focused on the cohesiveness or contagion of the original habitat type when it is the dominant landscape element (Franklin & Forman 1987; O'Neill *et al.* 1988; Ripple, Bradshaw & Spies 1991; Spies, Ripple & Bradshaw 1994; Wallin, Swanson & Marks 1994). These studies investigate potential restrictions on the movement of organisms, the spread of fire or disease, or the flow of nutrients at the landscape scale (Turner 1987; Turner *et al.* 1989; Bartell & Brenkert 1991; Turner & Dale 1991; Wiens *et al.* 1993; Ims 1995). The area of the original habitat generally is not measured when it is the dominant landscape element, because it forms one continuous patch and may extend beyond the defined landscape boundary. The area and distance between disturbance patches are nevertheless of interest because they serve as barriers to movement and affect the spatial configuration of the original habitat.

Our study focused on low fragmentation of forested landscapes, where the extent of forest has been altered by timber harvests but still comprises the dominant landscape element. We investigated the effects of habitat fragmentation on the American marten *Martes americana* Rhoads, a carnivorous mammal typically associated with mature forest systems. American martens appear sensitive to habitat fragmentation, because populations generally are low in areas fragmented by the clearcut method of timber harvest (Soutiere 1979; Snyder & Bissonette 1987; Thompson & Harestad 1994). However, marten responses to gradual increases in fragmentation are not well known. Most studies of timber harvest effects have been in areas where levels of fragmentation were not differentiated and where fragmentation was quite high, between 41% and 60% clearcut (Soutiere 1979; Steventon & Major 1982; Snyder & Bissonette 1987; Katnik, Harrison & Hodgman 1994; Thompson 1994; Potvin & Breton 1997). In our investigation, we were primarily interested in the response of martens to a gradual increase in fragmentation when forest connectivity was maintained, and therefore focused our study on a series of forested landscapes where non-forest cover ranged from 2% to 42%.

Brainerd (1990) proposed a model of marten response to fragmentation when non-forest cover occupied 55% of a hypothetical landscape. He predicted that habitat quality would increase if cut sizes were fine-grained, permitting marten movements across the clearcuts while taking advantage of increased prey in open areas. Habitat quality was predicted to decrease with medium- and coarse-grained cut sizes because they would restrict marten movements. A similar model was later developed by Thompson & Harestad (1994) that echoed Brainerd's (1990) predictions. Examining the full range of potential fragmentation, they predicted two possible changes in marten carrying capacity with increasing removal of timber. Under the clearcut method of harvest, equivalent to Brainerd's (1990) medium-grained or coarse-grained cut sizes, they predicted a linear negative decline. With selective cutting and patch cuts <3 ha, they predicted an increase in carrying capacity at low cutting levels, followed by a precipitous decline at approximately 20–30% of forest cover removal, due to increased predation of martens in openings, high edge density, and loss of forest interior. Thus, their model differed from Brainerd's (1990) only in predicting a decline at an earlier stage of fragmentation.

Although martens avoid clearcuts and other large openings, especially in the winter (Soutiere 1979; Clark & Campbell 1979; Steventon & Major 1982; Hargis & McCullough 1984), low levels of fragmentation may have little effect on martens as long as forest connectivity is maintained. In fact, a positive response to low fragmentation may be expected, because in some locales martens forage in brushy clearcuts during summer (Steventon & Major 1982; Katnik 1992) and hunt along forest–meadow edges (Simon 1980; Spencer, Barrett & Zielinski 1983). Having a small proportion of the landscape in open areas may be favourable to martens because of the increase in abundance and diversity of small mammals associated with clearcuts, and because marten diets are not restricted to forest-associated prey (Weckwerth & Hawley 1962; Koehler & Hornocker 1977; Buskirk & MacDonald 1984). The initial positive response would be followed eventually by a negative response as forested habitat became limiting.

To test these predictions, we compared marten capture rates across a series of increasingly fragmented landscapes. Our main objective was to determine whether marten abundance changed with incremental increases in habitat fragmentation caused by the combined effects of natural openings and timber clearcuts. If a correlation was found between capture rates and fragmentation, our secondary objective was to look for specific levels of fragmentation that suggested shifts in habitat quality in either a positive or negative direction. Preliminary results from this study were reported in Hargis & Bissonette (1997). This paper reports further analyses on the effects of landscape pattern on martens as measured by several landscape metrics.

Methods

SELECTION OF STUDY SITES

We selected 18 sites in the Uinta Mountains of northern Utah where martens were known to occur. Each site was a square area covering 9 km^2, a size chosen to ensure that several martens potentially could be present at any given time, yet sufficiently small to allow a thorough survey of marten numbers. Open areas occupied 2–42% of each site (Fig. 1). Natural openings in the form of meadows and boulder fields covered 2–12% of the landscapes, while timber harvests accounted for 0–42% of each site (Table 1).

All sites were located in mature forests containing Engelmann spruce *Picea engelmannii* Parry ex Engelm., lodgepole pine *Pinus contorta* Dougl. ex Loudon and scattered subalpine fir *Abies lasiocarpa* [Hook.] Nutt., with canopy cover >30%, large diameter trees, and abundant coarse woody debris (Table 2). Elevations ranged from 2700 to 3200 m. Similarity in vegetative conditions was important to minimize variation among sites from factors other than fragmentation.

We limited our study to the clearcut method of timber harvest, because marten responses to selective cutting may differ (Thompson & Harestad 1994). We chose sites where clearcutting had occurred at least 5 years before to maximize the possibility of a stable marten response relative to this disturbance. However, one site contained cut blocks <2 years old, and two sites contained clearcuts that had been harvested the previous year, but these totalled <2% of each landscape.

In most cleared openings, average tree heights were <2 m because of planting failures and slow growth at high elevations. Dominant vegetation was grasses and forbs, providing a distinct contrast with adjacent forests. Harvested areas lacked coarse woody debris because logging slash was normally piled and burned.

Our investigation involved four parts: estimation of marten use within each site, quantification of landscape fragmentation, estimation of potential prey abundance and characterization of forest structure. The first two aspects were associated directly with the question of forest fragmentation effects on the American marten. The latter two assessed whether factors other than fragmentation contributed to differences in marten use among sites.

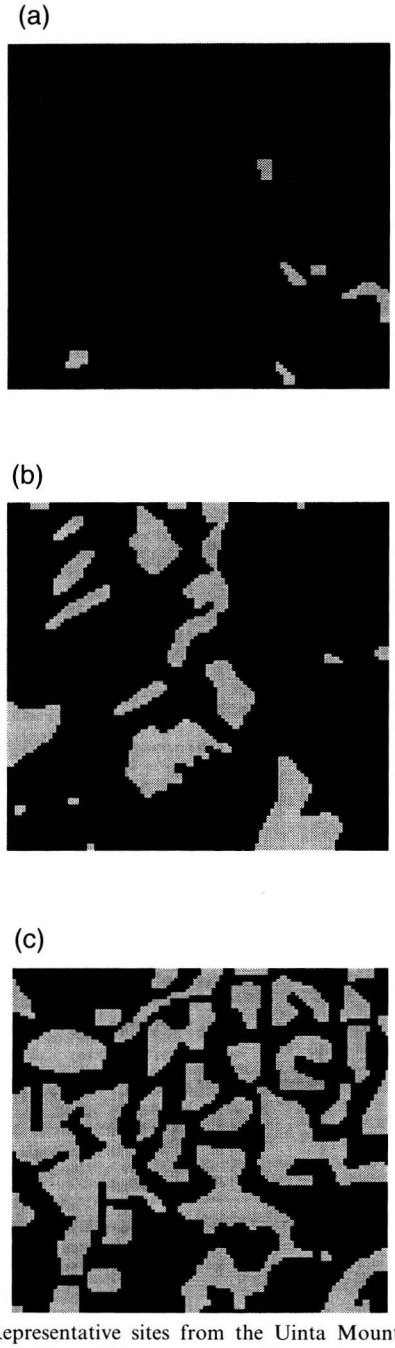


Fig. 1. Representative sites from the Uinta Mountains of northern Utah used in the study of forest fragmentation effects on the American marten: (a) Beaver Meadow (b) Hayden Pass and (c) East Park. Black represents forest and grey represents open areas.

ESTIMATION OF MARTEN USE

We used summer capture rates of individual martens, excluding recaptures, as a means of comparing marten use at each site. Twenty-five live traps were placed in a systematic grid covering each entire site (750 m spacing) and were monitored for 6 consecutive nights. This design potentially yielded 150 trap nights per site, but actual trapping effort varied among sites due to trap disturbance, damage and other field conditions. Each site was sampled at least once during four trapping periods between 1991 and 1993. We surveyed nine sites twice in separate years to examine potential differences in capture rates between years, and one site was surveyed in all three summers. To examine potential differences in capture rates from early to late summer, we resurveyed four sites twice during the same summer. Captured martens were sedated with ketamine, weighed and ear-tagged. We recorded the weight, gender, and overall body condition of each

Table 1. Landscape characteristics of 18, 9-km^2 landscapes in the Uinta Mountains of Utah

Site	% of site in openings*	% of site in clearcuts	Edge density	Mean proximity index	Nearest neighbour distance	Mass fractal dimension
Beaver†	1·7	0·0	5·0	3·7	523	1·99
Anderson	4·6	3·4	11·1	10·8	181	1·98
Highline	5·8	2·9	13·2	0·8	370	1·99
Spirit	7·6	0·0	14·3	2·3	252	1·98
Sims	8·3	5·0	19·3	9·9	102	1·97
Marsh East	9·1	8·9	17·6	36·6	224	1·97
Bull	9·9	0·0	17·6	23·4	337	1·96
Manila	14·2	9·9	24·6	21·6	150	1·96
Sheep	14·3	11·2	24·7	97·8	118	1·97
Cliff	15·6	3·3	28·3	39·0	132	1·96
Chepeta	16·7	12·1	34·0	43·7	83	1·94
Hayden†	16·8	10·5	26·8	10·6	216	1·93
Dahlgreen	19·5	18·4	39·4	25·2	95	1·92
Deer	21·6	15·2	39·4	28·3	123	1·89
Marsh West	25·3	19·6	35·2	106·7	84	1·91
Long Park	36·1	31·2	52·5	149·4	99	1·86
Gold	39·1	8·8	50·3	305·5	75	1·84
East Park†	41·9	41·9	64·2	169·8	62	1·78

* Natural openings and clearcuts combined to form two-attribute landscapes.
† Illustrated in Fig. 1.

Table 2. Forest structure characteristics of lodgepole pine–spruce forests in 18 sites in the Uinta Mountains of Utah. Variables above the dashed line were similar among sites (Fig. 2)

Structural attribute	Mean	Standard deviation
Basal area (m^2 ha^{-1})	37	5
Overstorey basal area (m^2 ha^{-1})	29	5
Canopy cover (%)	45	8
Stand density index	839	141
Stand $d.b.h._q$ (cm)	22	3
Diameter of sound logs (cm)	18	2
Diameter of rotten logs (cm)	21	3
Metric tons ha^{-1} of sound logs	15·3	8·6
Metric tons ha^{-1} of rotten logs	18·2	10·9
Overstorey $d.b.h._q$ (cm)	27	6
Overstorey lodgepole pine $d.b.h._q$ (cm)	19	5
Overstorey spruce $d.b.h._q$ (cm)	15	11
% of live overstorey in lodgepole pine	61	25
% of live overstorey in spruce	25	18
Live crown ratio of overstorey trees	51	13
% of total stems in snags	29	15
% of overstorey stems in snags	34	19
% of basal area in snags	35	18
% of overstorey basal area in snags	36	20

marten, and noted the appearance of lactation in females.

Because high capture rates do not necessarily imply high quality habitat (van Horne 1983; Pulliam 1988), we used reproductive status, weight, body condition and recapture in subsequent years to assess whether high capture rates were generally associated with other indicators of good health and reproduction. This information was qualitative because sample sizes were insufficient for statistical analyses.

Martens were not harvested commercially during our study. A 5-year moratorium on commercial trap-

ping of martens in the Uinta Mountains was initiated in 1990, one trapping season prior to the onset of our study. Additionally, no trapping had occurred in the 2 years prior to the moratorium (Utah Division of Wildlife Resources, unpublished data), and prior to that there had been sporadic harvesting by only two trappers, most of which occurred outside our study sites.

ANALYSIS OF FRAGMENTATION

We obtained raster images of our study sites by extracting the relevant areas from an existing vegetation map of the Uinta Mountains. The vegetation map was derived from LANDSAT TM data (30-m resolution) and had been classified into 35 vegetation types with corrections for slope, aspect and elevation (Homer *et al.* 1997). Our extracted images contained 12 of the 35 vegetation types, and we aggregated these into two classes: forests and open areas (clearcuts and natural openings combined). We reduced mapping error by comparing the classified images to aerial photos, and corrected all misclassified pixels to match the shapes of vegetation polygons on the photos.

We further simplified the maps to remove fragmentation 'noise' that occurred at a finer grain than perceived by martens. Assuming that martens readily cross 30-m openings (Koehler & Hornocker 1977; Hargis & McCullough 1984), patches <30 m were removed by blending all single pixel openings with the surrounding forest polygon. Likewise, isolated forest pixels were reclassified to match the clearcut or natural opening in which they occurred.

We quantified habitat fragmentation using five measures: the percentage of landscape in openings, edge density (m ha^{-1}), mean proximity index, mean nearest-neighbour distance between open areas (m), and mass fractal dimension. The first five measures were calculated with a spatial pattern analysis program, FRAGSTATS (McGarigal & Marks 1995). Mass fractal dimension was calculated using software developed by B. Milne and T. Keitt at the University of New Mexico.

We calculated the percentage of landscape in openings as the combined percentages of clearcuts and natural openings within each study site. Edge density was the sum of all edge pixels divided by total landscape area, expressed as metres of edge per hectare.

Mean proximity index quantified the mean isolation of each open patch from all other openings within a specified search radius, taking into account the size of all other openings as well as the distance between them. The mean proximity index was derived from individual proximity indices for each patch in the landscape, when each patch is viewed as a 'focal patch'. The proximity index for each patch was calculated as the sum, for all patches within the search radius of the focal patch, of patch area (m^2) divided by nearest edge-to-edge distance squared (m^2) (McGarigal & Marks 1995, modified from Gustafson & Parker 1992). High values of the mean proximity index indicated closer proximity between open patches. We used the full extent of each study site (3000 m) as the search radius for each patch.

We calculated mean nearest-neighbour distance between openings as the average edge-to-edge distance between each non-forested patch in the landscape and its nearest neighbour. This measure differed from the proximity index by ignoring patch size and by defining interpatch distance only with the nearest open patch. Mean nearest-neighbour distance yields an absolute value that only can be used to compare landscapes with the same extent and resolution (Gustafson & Parker 1992), but our sites met these criteria.

Mass fractal dimension was used to describe the fractal nature of the forest matrix. We chose this fractal measure over a perimeter-area fractal because it characterized the shape of the forest matrix caused by placement of open patches, rather than measuring the irregularity of individual patch perimeters. Mass fractal dimension represents the scaling relationship between the average number of forested pixels contained within a subsample of a landscape and the length of the box defining the subsample. Computationally, it is the slope derived from the log of the average number of pixels associated with a series of increasing box sizes regressed on the log of the box lengths (Voss 1988; Milne 1991). We calculated mass fractal dimension by counting the mean number of forested pixels in subsamples of the landscape contained within square boxes with edge lengths of 3, 9, 15, 21 and 27 pixels. Theoretical limits of this measure are between 0 and 2. A value of 2 is achieved when the forest completely fills the 2-dimensional landscape, and is reduced to some dimension <2 as non-forest patches are added.

ESTIMATION OF PREY DENSITY

We estimated small mammal populations on 12 of the sites during a 7-week snap-trap survey between 22 July and 8 September 1992. Each site was surveyed with 12 trap lines consisting of 16 stations spaced 20 m apart, with each station consisting of 2 Victor mouse traps and 1 Victor rat trap, except for the last station which had one mouse and one rat trap. Lines were placed in forested areas, clearcuts and meadows in approximate proportion to the availability of each of the three habitat types, and were run for 2 nights (1200 trap nights per site). Actual trap nights were calculated by subtracting all traps that malfunctioned or were sprung each night. We estimated the relative abundance of each species as captures per 100 trap nights, and calculated total biomass of mammals per line from measured weights. Data were summarized by site and by habitat types within each site.

ANALYSIS OF FOREST STRUCTURE

Various aspects of forest structure appear important to martens, particularly a fairly closed canopy and

abundant coarse woody debris (reviewed by Buskirk & Powell 1994). To determine whether marten capture rates might be influenced by forest structure, we measured structural attributes of forested habitat within each site. Using a modified plotless cruise at 25 points, mean values were derived for 19 structural variables for each site. Points were located at random compass directions and random distances 1–30 m from each marten trap. For marten traps located in openings or at the edge of openings, points were randomly selected within the nearest forest. We used a basal area prism to establish the number of trees included within the point sample, and recorded height, diameter at breast height (d.b.h.), species, crown class, live crown ratio and snag decay class of each tree included. Live crown ratio was a visual estimate of the percentage of total tree height in live branches. We identified two crown classes: understorey and overstorey, and seven snag decay classes based on Thomas (1979). Live trees with dead tops (snag class 2) were classified as snags rather than live trees.

We calculated the stand density index (Reineke 1933) as the relationship between quadratic mean diameter (d.b.h.$_q$) and trees per ha (t.p.h.) using the formula SDI = t.p.h. (d.b.h.$_q$/25)$^{1.6}$ (Daniel & Sterba 1980). We estimated the amount of conifer reproduction by tallying all trees <7 cm d.b.h. within four 2-m radius plots located five paces from each sampling point in the cardinal directions. Canopy cover was measured with a densiometer at the centre of these four plots.

We determined abundance of coarse woody debris by establishing two 15-m transect lines that extended from the plotless cruise sampling point in random directions (Brown 1974). We recorded the diameter of all woody material >10 cm intersecting the lines and classified woody debris as being either sound or rotten. We calculated biomass density (kg ha^{-1}) for sound and rotten decay classes, using formulae developed by Brown (1974).

STATISTICAL ANALYSES

At the end of the 3-year survey period, we had surveyed each of the sites 1–3 times out of four possible sampling periods. Because repeated trapping efforts within each site were not independent, we used a bootstrap technique (Efron & Tibshirani 1993) to select randomly one trapping effort from each site, including the number of individual martens caught and total trap nights for that trapping effort. We repeated this procedure to generate 35 unique combinations of trapping efforts, each containing one trapping effort per site ($n = 18$ for all 35 data sets). This procedure enabled us to mix capture results from all years and from early or late summer seasons in a variety of combinations.

We used Poisson regression analysis (Frome, Kutner & Beauchamp 1973) to test for differences in marten capture rates among sites due to fragmentation, prey availability and forest structure. The analysis was run on all 35 data sets, and from this an average P-value and 95% confidence interval (CI) was calculated. We chose the Poisson model because marten captures were counts that occurred at a low rate, and the data most closely fit the Poisson distribution. Our data were overdispersed, leading us to use a quasi-likelihood method for estimating model parameters, and a χ^2 statistic was used to test for significance of these parameters (McCullagh & Nelder 1989).

We tested five fragmentation models, one for each measure described in the section on fragmentation, and evaluated the relative strength of each model based on a comparison of R^2-values. We did not generate a model containing all fragmentation variables because initial data exploration revealed high correlation among measures. We were interested, however, in determining whether any of the measures were more strongly correlated with marten numbers than others.

Prior to conducting the regression analysis, we evaluated 18 measures of forest structure and seven variables from the small mammal survey to determine whether there were sufficient differences among the sites, in either forest structure or prey abundance, to warrant inclusion in the analysis of fragmentation. Due to the large number of these variables relative to the sample size of landscapes, we used data exploration techniques to eliminate variables that either did not appear to differ among sites, or that differed but were not correlated with marten captures. We examined box plots for each variable for differences among sites, and where differences were observed we used correlation coefficients between each variable and marten captures to determine whether the variable should be added to the fragmentation models.

Results

INFLUENCES OF FOREST STRUCTURE AND PREY AVAILABILITY

Nine forest structure variables showed close similarity among sites, and 10 variables differed, based on exploratory analysis using box plots (Table 2). Canopy cover and several measures of coarse woody debris were among the variables that were similar among sites (Table 2 and Fig. 2). None of the forest structure measures was strongly correlated with marten captures, and only the measures of snag abundance had correlation coefficients $>|0{\cdot}20|$ (Table 3). Based on a forward stepwise regression of the 10 variables that differed among sites and marten captures, only percentage of total stems in snags (henceforth called snag abundance) explained sufficient variation in marten captures to be included in subsequent models of fragmentation, and all other forest structure variables were dropped from further analysis.

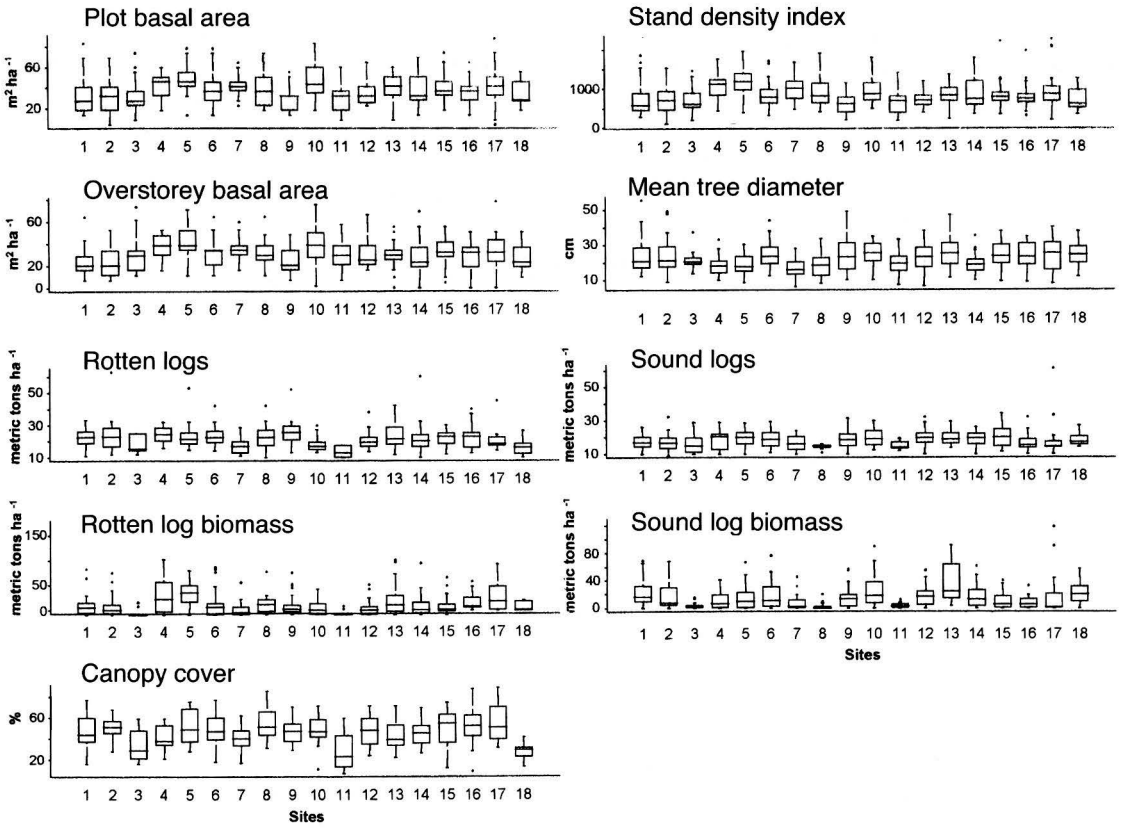


Fig. 2. Box plots for forest structure variables having similarity among sites, with sites arranged from highest to lowest marten capture rates. The solid line in the box represents the median value, the box defines the first and third quartiles, and extreme values are shown as dots.

Table 3. Pearson correlation coefficients between marten capture rates and forest structure variables, with coefficients $>|0{\cdot}20|$ highlighted in bold

Variable	r
Basal area (m^2 ha^{-1})	−0·17
Stems ha^{-1}	0·01
Stand density index	−0·10
Canopy cover	0·00
Live crown ratio of overstorey trees	0·04
Stand $d.b.h._q$ (cm)	−0·15
Overstorey dbh_q (cm)	0·15
Overstorey lodgepole pine $d.b.h._q$ (cm)	0·11
Overstorey spruce $d.b.h._q$ (cm)	0·05
% of live overstorey in lodgepole pine	−0·02
% of live overstorey in spruce	0·04
% of total stems in snags	**−0·52**
% of basal area in snags	**−0·44**
% of overstorey stems in snags	**−0·48**
% of overstorey basal area in snags	**−0·42**
Diameter of sound logs	−0·02
Diameter of rotten logs	0·02
Metric tons ha^{-1} of sound logs	−0·04
Metric tons ha^{-1} of rotten logs	0·15

Because of the negative correlation between snag abundance and marten captures, we explored correlations of other variables with snag abundance. We found a positive relationship between snag abundance and the percentage of site in clearcuts ($F = 6{\cdot}54$, d.f. = 1,16, $P = 0{\cdot}02$, $R^2 = 0{\cdot}25$) and a negative correlation between snag abundance and canopy cover ($F = 10{\cdot}85$, d.f. = 1,16, $P = 0{\cdot}005$, $R^2 = 0{\cdot}37$). Marten captures, however, were not correlated with canopy cover ($r = -0{\cdot}01$), because cover was within an acceptable range for marten habitat suitability at all sites. Canopy cover ranged from 28% to 55%, and a lower limit of 30% is considered suitable (Koehler & Hornocker 1977; Spencer, Barrett & Zielinski 1983). There was no significant correlation between snag abundance and biomass density of coarse woody debris ($F = 0{\cdot}15$, d.f. = 1,16, $P = 0{\cdot}70$, $R^2 = 0{\cdot}0$) or between snag abundance and vole densities ($F = 1{\cdot}29$, d.f. = 1,16, $P = 0{\cdot}27$, $R^2 = 0{\cdot}02$).

The small mammal survey resulted in 1753 captures in 11 417 trap nights, excluding sprung traps. The five most commonly trapped species were the southern red-backed vole *Clethrionomys gapperi* Merriam, deer mouse *Peromyscus maniculatus* Osgood, Uinta chipmunk *Eutamias umbrinus* J. A. Allen, least chipmunk *Eutamias minimus* A. H. Howell, and the vagrant/masked shrew complex *Sorex vagrans* Merriam and *S. cinereus* Kerr. We investigated seven variables that related to prey availability: captures per 100 trap nights for each of the five common species (five variables); total biomass per trap nights of all mammals

captured per site; and total captures per 100 trap nights per site. Total biomass was the total weights of all mammals trapped per site, excluding the weights of incidental snap-trap captures of snowshoe hare *Lepus americanus* Erxleben. We found differences among sites for all prey variables, but all were weakly correlated with marten captures (Fig. 3 and Table 4). Vole captures showed the highest correlation with marten captures ($r = 0{\cdot}72$) but were not a significant predictor of marten captures either when used alone (mean P of 35 bootstrap samples = 0·68, CI = 0·65, 0·71) or in combination with one of the fragmentation measures and snag abundance (mean P of 35 bootstrap samples = 0·53, CI = 0·50, 0·56). The correlation between marten and vole captures was primarily due to one site that had both the highest number of martens and an extremely high density of voles (Fig. 4b). When this site was omitted, the correlation coefficient was 0·53.

Although prey availability was not correlated with marten captures, we found differences in prey among forests, meadows and clearcuts that were useful in interpretation of marten response to fragmentation. The

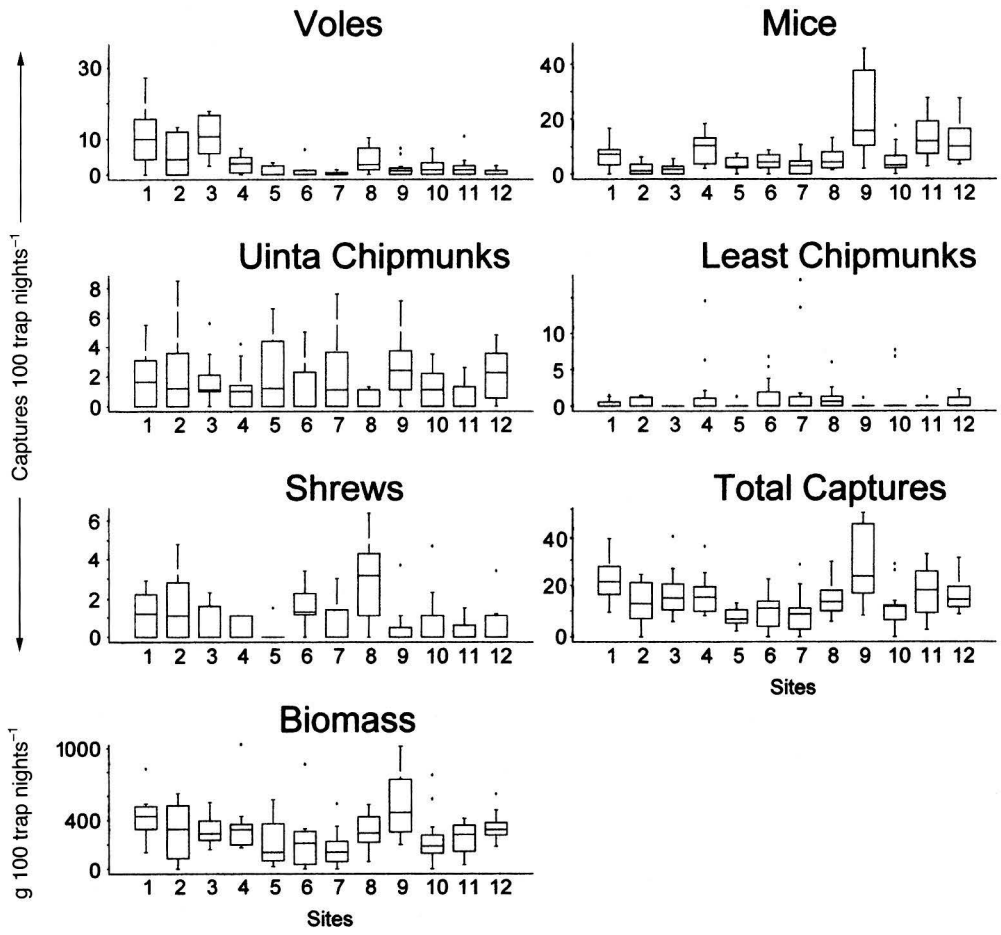


Fig. 3. Box plots for prey variables, with sites arranged from highest to lowest marten capture rates. The solid line in the box represents the median value, the box defines the first and third quartiles, and extreme values are shown as dots.

Table 4. Pearson's correlation coefficients between marten capture rates and prey variables

Variable	r
Voles 100 trap nights^{-1}	0·72
Deer mice 100 trap nights^{-1}	−0·37
Uinta chipmunks 100 trap nights^{-1}	0·21
Least chipmunks 100 trap nights^{-1}	−0·14
Shrews 100 trap nights^{-1}	0·12
Total mammals 100 trap nights^{-1}	0·16
Biomass 100 trap nights^{-1}	0·29

density of small mammals was highest in clearcuts, followed by forests and meadows (χ^2 for clearcuts vs. forests = 20·12, d.f. = 1, $P = 0{\cdot}001$; χ^2 for meadows vs. forests and clearcuts = 16·14, d.f. = 1, $P = 0{\cdot}001$). We captured an average of 21 mammals 100 trap nights^{-1} in clearcuts, 14 mammals 100 trap nights^{-1} in forests, and 6 mammals 100 trap nights^{-1} in meadows. The total biomass was highest in clearcuts, followed by forests and meadows ($F = 17{\cdot}5$, d.f. = 2, $P < 0{\cdot}001$).

MARTEN RESPONSE TO FRAGMENTATION

We captured 53 individual martens (34 males and 19 females; 46 adults and 7 juveniles) in 4983 trap nights,

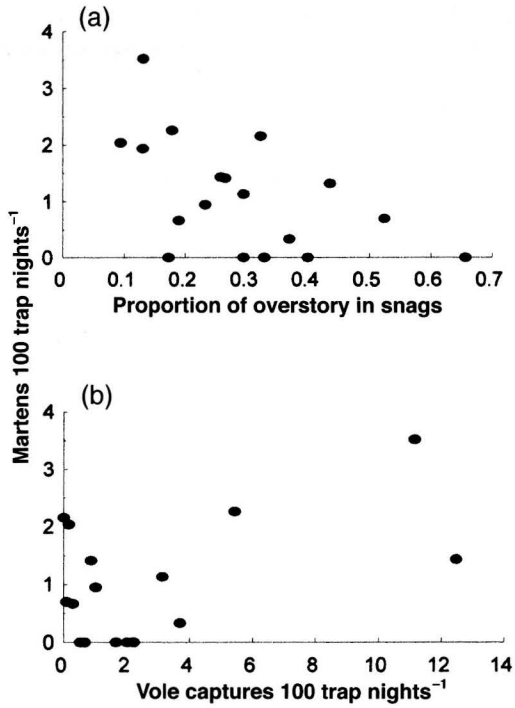


Fig. 4. Scatterplot of individual marten captures with (a) percentage of total stems in snags and (b) vole captures 100 trap nights^{-1}.

with 0–8 individual captures per site during any given trapping period. Although capture rates differed among sites (described below), we found no significant difference in capture rates among trapping periods within any given site ($\chi^2 = 2{\cdot}89$, d.f. = 3, $P = 0{\cdot}41$). Sites with high captures were consistently high, and sites with zero captures remained low, resulting in a nearly stable ranking of sites across all years, and confirming that differences in capture rates were due to factors other than seasonal variation or sampling error.

Marten captures were negatively correlated with loss of forest habitat, as measured by the percentage of each site in open areas, and this relationship was significant ($P = 0{\cdot}03$) when snag abundance was added to the model (Table 5). Capture rates were variable in sites with low fragmentation, but only one marten was captured in 937 trap nights in the four sites having >0·25% open areas (Fig. 5a).

Martens showed significant responses to landscape pattern as well as loss of habitat (Fig. 5b–d and Table 5). Capture rates were lowest in landscapes with large, closely spaced open areas, as measured both by mean proximity index and nearest-neighbour distance. Landscapes with an average distance between open areas <100 m had no marten captures. Also, landscapes with high edge density had fewer marten captures. We did not observe a significant correlation between marten captures and mass fractal dimension, although the trend was for low to zero captures in landscapes where the forest matrix was highly convoluted (Fig. 5e and Table 5).

We examined correlations between percentage of each site in openings and the four measures of landscape pattern to assess the degree of additional information provided by these measures (Table 6). Correlations were generally high, with mass fractal dimension having the highest correlation with habitat loss ($r = -0{\cdot}97$) and nearest-neighbour distance the lowest ($r = -0{\cdot}67$). In addition, the four measures were interrelated among themselves, with edge density and mass fractal dimension having the strongest correlation ($r = -0{\cdot}96$).

Partly as a consequence of these interrelationships, nearest-neighbour distance, edge density and percentage of site in openings were similar in their role as explanatory variables of marten capture rates. Used alone, each explained approximated 20% of the variation in marten capture rates and *P*-values were similar. When used in combination with snag abundance, percentage of site in openings and edge density became better predictors, but the relationships for nearest-neighbour distance were weakened. Mass fractal dimension provided the poorest fit of all fragmentation measures examined, both when used alone or in combination with snag abundance.

The combined effects of mean proximity index and snag abundance provided the best fit for explaining differences in marten capture rates, based on a comparison of *P*-values and R^2 terms from all fragmentation models examined (Table 5). The contribution of mean proximity index was greater than that of percentage of site in openings, which became an insignificant term when both measures were included in a model (mean *P* for each variable, respectively, based on 35 bootstrap runs = 0·37 and 0·01).

Discussion

Martens appeared to respond negatively to low levels of habitat fragmentation, based on a significant decrease in capture rates observed across a series of increasingly fragmented landscapes. Martens were rarely detected in sites with >25% open areas, even though forest connectivity was still present.

Martens were sensitive not only to loss of habitat but also to the size and proximity of open areas. As measured by the mean proximity index, marten capture rates decreased as open patches became more closely situated (Fig. 5b). When the average nearest-neighbour distance between open patches was <100 m, nearly all forest interior had been converted to narrow strips of forest that functioned only as edge habitat (Fig. 1c).

We provide several caveats to aid in interpreting these results. First, R^2 values associated with all significant relationships were low. It may be unrealistic to expect high R^2 values in a study design where landscapes are the units of replication, but nevertheless

Table 5. Statistical significance of fragmentation models explaining individual marten capture rates, with mean *P*-values (confidence intervals in parentheses) derived from chi-square tests performed on 35 bootstrap data sets per model (error d.f. = 15 in each model). Models with $P < 0.05$ are indicated with an asterisk. The second column contains both the mean univariate *P*-value and the mean multivariate *P*-value of the fragmentation measure when snag abundance is added to the model

Model parameters	*P*-value of fragmentation measure	*P*-value of snag abundance in multivariate model	R^2
% of site in openings	0·06 (0·05, 0·07)		0·23 (0·21,0·25)
* % of site in openings, snag abundance	0·03 (0·02, 0·04)	0·01 (0·01, 0·01)	0·50 (0·48, 0·52)
* Proximity index	0·01 (0·01, 0·01)		0·48 (0·47, 0·49)
Proximity index, snag abundance	0·04 (0·03, 0·05)	0·07 (0·06, 0·08)	0·59 (0·58, 0·60)
* Nearest-neighbour distance	0·03 (0·03, 0·03)		0·21 (0·20, 0·22)
* Nearest-neighbour distance, snag abundance	0·05 (0·02, 0·08)	0·03 (0·01, 0·05)	0·42 (0·40, 0·44)
Edge density	0·08 (0·07, 0·09)		0·19 (0·17, 0·21)
* Edge density, snag abundance	0·05 (0·01, 0·09)	0·01 (0·00, 0·02)	0·47 (0·45, 0·49)
Mass fractal dimension	0·12 (0·10, 0·14)		0·17 (0·15, 0·19)
Mass fractal dimension, snag abundance	0·11 (0·04, 0·18)	0·02 (0·01, 0·03)	0·43 (0·39, 0·47)

the low R^2 values indicate substantial unexplained variation in marten capture rates.

Secondly, the size chosen for study areas was small relative to marten home range scale. The size of marten home ranges in the Uinta Mountains is unknown, but in the neighbouring state of Wyoming the mean summer home ranges (95% minimum convex polygon) of seven females was 669 (±67 SE) ha and that of eight males was 1820 (±153 SE) ha (O'Doherty, Ruggiero & Henry 1997), sizes that would suggest only 1–2 martens per landscape. Nevertheless, we expected several martens to occur in each landscape because home range boundaries were unlikely to correspond to study area boundaries, and therefore partial home ranges of several martens could be represented. Martens exhibit intrasexual territoriality (reviewed by Powell 1994) but >1 female range typically occurs within those of males. Non-territorial juveniles sometimes share ranges with territorial adults (Archibald & Jessup 1984). Rather than view these landscapes from a home range perspective, we viewed each landscape as a window providing a snapshot of marten numbers at a given point in time.

A third caveat is that marten capture rates represent relative, not absolute, marten numbers. Sites with no marten captures may have contained martens but at densities too low to detect during the 6-night trapping period. To increase our confidence in interpreting zero values, we resampled all sites in which no martens were caught, and in all cases no martens were captured during these second attempts. Nevertheless, we cannot conclude that no martens were present.

Also, we were unable to determine whether martens in our samples were residents or transients. This is an important consideration because high numbers of transients could indicate a population sink (Pulliam 1988). Although we do not know how many transients occurred in each site, we do know that sites with high marten captures contained residents. The two sites with the highest number of captures were the only sites where we recaptured the same individuals in subsequent years. These sites also represented two of the four sites with lactating females, denoting reproductive activity. In the site with the highest capture rate, the average weight of males was above average for all sites, and general body condition was fair to excellent. Thus, there is no evidence to suggest that sites with high captures were simply areas of dispersal.

Our final caveat regards the apparent threshold in marten occurrence when open areas were approximately 25% of the total landscape. Martens in our sites may have exhibited a stronger response to low levels of fragmentation than would be expected in geographical areas with less harsh conditions. The clearcuts in our sites provided no habitat for martens because cut areas generally were stripped of both vegetation and logging slash after timber harvest. Moreover, the top soil was considerably disturbed, often

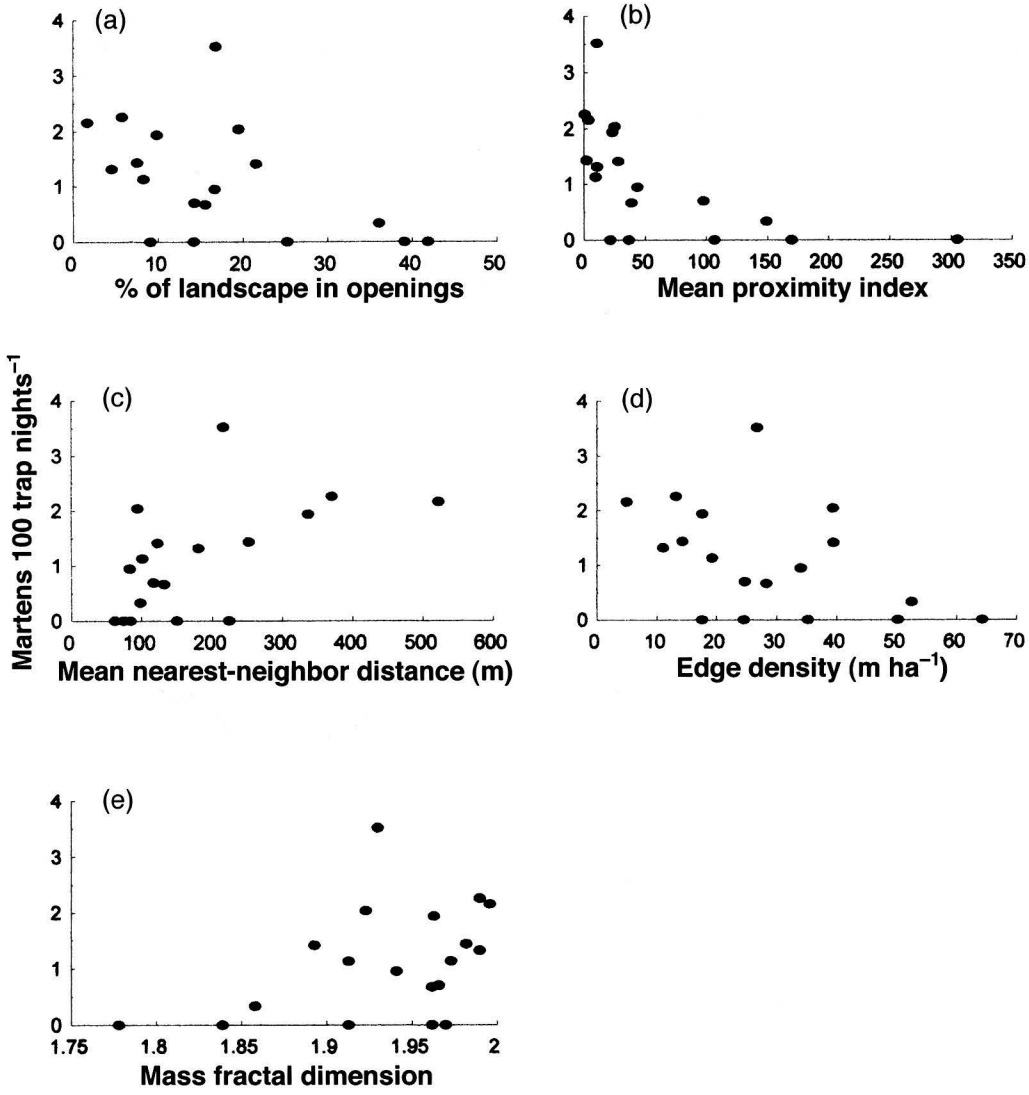


Fig. 5. Scatterplot of marten capture rates with five measures of fragmentation: (a) percentage of site in openings; (b) mean proximity index; (c) mean nearest-neighbour distance; (d) edge density; and (e) mass fractal dimension.

Table 6. Correlation matrix for landscape metrics and snag abundance, with all coefficients >|0·70| highlighted in bold

	Marten	% open	Edge density	Proximity index	Nearest neighbour distance	Mass fractal dimension	Snags
Marten	1·00	−0·50	−0·45	−0·59	0·56	0·41	−0·53
% open		1·00	**0·97**	**0·85**	−0·67	**−0·97**	0·28
Edge			1·00	**0·74**	**−0·72**	**−0·96**	0·26
Proximity index				1·00	−0·50	**−0·79**	0·28
Nearest-neighbour distance					1·00	0·59	−0·26
Mass fractal dimension						1·00	−0·32
Snags							1·00

retarding the establishment of conifer growth for a decade or more.

Elsewhere, martens apparently can forage in clear-cuts containing structure in the form of regenerating deciduous or conifer vegetation and brush (Steventon & Major 1982; Katnik 1992; Potvin & Breton 1997) and may tolerate higher levels of fragmentation under these circumstances. Soutiere (1979) found marten using areas that were 60% cut in Maine, although at lower population levels than in uncut areas. We find it

noteworthy, however, that Chapin & Harrison (1998), working in the same general vicinity as Soutiere, found no adult female marten territories where >31% of the landscape was in regenerating vegetation. The median percentage of home range area in regenerating patches was 20% for 14 resident adult females and 22% for 13 resident adult males (Chapin & Harrison 1998). Also, Thompson (1994) found resident marten at only one of five sites with logged forests, and clearcuts on these sites were vegetated with shrubs and quaking aspen *Populus tremuloides*. These studies indicate that marten residency, if not marten presence, may be affected by fairly low levels of fragmentation, regardless of the vegetation present in open areas. In areas where openings are poorly vegetated for long periods, we anticipate that martens would respond to fragmentation at approximately the same level that we observed. For example, clearcut management comparable to that of the Uinta Mountains occurs in much of the lodgepole pine and spruce forests of the intermountain states of western North America, and we consider our results relevant to marten conservation in that geographical area.

Our findings may be pertinent to the conservation of the Eurasian pine marten *Martes martes* Linnaeus as well. Of 46 British mammals analysed for vulnerability to fragmentation, the pine marten was considered one of the most vulnerable due to relatively low population density, slow breeding, fairly poor dispersal capabilities and close affinity to semi-natural habitats (Bright 1993). In the former USSR, notable declines in marten abundance were apparent when mature forest was reduced to 25–35% of total area (Grakov 1972). In northern Sweden, pine marten densities were found to be two to three times higher within an old-growth forest reserve than in the surrounding landscape of commercially managed, fragmented forest (Bjärvall, Nilsson & Norling 1977; cited in Brainerd 1997). In southern Sweden and south-eastern Norway, pine martens consistently preferred later-successional seres of spruce-dominated forest and avoided open habitats throughout the year (Brainerd 1997).

Martens in Scotland appear to tolerate high levels of forest fragmentation, but Balharry (1993) found that the normal rodent diet is supplemented by carrion, mostly from red deer *Cervus elaphus* culling operations and, to a lesser extent, from hill sheep *Ovis aries*. Carrion accounted for 35% of the estimated weight intake of all marten foods in two study sites. Nevertheless, some minimum area of woodland seemed important for establishing breeding territories, because breeding adults had significantly more woodland in their territories than juveniles and non-breeding adults (Balharry 1993). In a comparison of two study sites in Scotland, Balharry (1993) found that male marten home ranges were three times larger in the site having only 3·5% woodland than in the site with 27% woodland.

American martens may be somewhat more sensitive to fragmentation than pine martens, and may require a certain proportion of forest interior within their home ranges. As summarized by Buskirk & Powell (1994), martens appear to use structural components of mature forests to avoid predators (Drew 1995), to gain access to prey in winter (Hargis & McCullough 1984; Corn & Raphael 1992; Sherburne & Bissonette 1993; Sherburne & Bissonette 1994) and to gain thermal advantages, especially while resting (Buskirk *et al.* 1989; Taylor 1993; Raphael & Jones 1997). Each of these could be affected by loss of forest interior habitat. Forest patches <100 m wide may not provide sufficient escape cover from known predators such as red fox *Vulpes vulpes*, coyote *Canis latrans* and raptors (Hodgman *et al.* 1997; Thompson 1994). Availability of preferred prey may also be a factor. Mills (1995) found lower densities of California red-backed voles *Clethrionomys californicus* near edges than in forest interiors, and Nordstrom (1995) found lower densities of southern red-backed voles in narrow forest corridors compared to contiguous forest blocks during a low population year. Thermal advantages may also be lost in forests that have been reduced to narrow strips. Chen, Franklin & Spies (1995) found that microclimatic edge effects can extend >240 m into old-growth Douglas-fir forests. Therefore, a forest interspersed with closely spaced open patches may lack the thermal conditions normally associated with mature forests due to landscape pattern.

Edge habitat *per se* is not necessarily detrimental to martens. Marten use of edge may depend on the habitat composition on either side (Buskirk & Powell 1994). In California, martens showed preferential use of edge that bordered mesic meadows (Simon 1980; Spencer, Barrett & Zielinski 1983) and in Maine edge between residual conifer forests and regenerating clearcuts was used in proportion to availability (Chapin 1995; Chapin & Harrison 1998). In our study, the correlation between edge density and mean proximity index made it difficult to determine whether martens responded negatively to edge, or whether the actual response was to the loss of forest interior from closely spaced patches, and edge was simply a covariate.

In addition to loss of interior habitat, martens may avoid landscapes with abundant openings due to the increased energetic costs of circumventing the open areas. It may be energetically prohibitive to defend a territory or forage in a home range that is widely diffused and interspersed with large patches of unsuitable habitat (Thompson & Colgan 1994).

We found no evidence that martens benefit from the increase in abundance and diversity of prey associated with clearcuts. We cannot state this conclusively because we did not collect dietary information, but our trapping data did not indicate a positive response to prey in clearcuts. Although small mammal densities were higher in clearcuts than in forest habitat, marten capture rates were not correlated with biomass of prey found in clearcuts, or with the abundance of any

species associated with clearcuts. Information on red squirrel (*Tamiasciurus hudsonicus* Trouessart) or snowshoe hare abundance, which we did not obtain, would not have changed the relationship between martens and clearcut-associated prey, because both are associated with forests (Raphael 1988; Thompson & Colgan 1994). Seven of the eight incidental captures of snowshoe hares were in forests.

We found a negative correlation between marten capture rates and snag abundance, but martens showed a positive response to snags in other studies (Spencer, Barrett & Zielinski 1983; Lofroth 1993; Drew 1995), partly because of their use of large diameter snags for resting sites (Campbell 1979; Spencer, Barrett & Zielinski 1983). In our study, snags were a common habitat feature in all sites and may not have been limiting to martens, but snag abundance varied among sites due to differences in mortality from mountain pine beetle *Dendroctonus ponderosae* Hopkins. The representation of snags in the overstorey ranged from 9% in an uninfected site to 65% in a heavily infected area. Sites with high beetle mortality were frequently selected for salvage timber harvests, and therefore sites with high snag densities also had the greatest number of clearcuts. Thus, the negative correlation between martens and fragmentation is mirrored by the negative correlation between martens and snag abundance. Because snag abundance improved the fit of all fragmentation models (Table 5), however, it is more than a correlate with fragmentation, and may be influencing marten ecology in ways that our data did not reflect. The more open canopy cover associated with high snag densities may cause edge effects to extend further into forests, causing a greater loss of forest interior at any given level of fragmentation than sites with low snag abundance.

RECOMMENDATIONS FOR MANAGEMENT AND RESEARCH

Our study was designed to assess changes in marten capture rates over a range of habitat fragmentation, but we were unable to separate the effects of habitat loss from the effects of landscape pattern. All measures of landscape pattern except mass fractal dimension were significantly correlated with marten captures, but each change in the measure of pattern was associated with a change in available habitat. To isolate the effects of landscape pattern, it would be necessary to sample martens in several landscapes having the same level of habitat loss but differing in landscape pattern. Landscapes with 20–35% of the area in openings appear fruitful for further investigations, based on the notable change in capture rates we encountered at this level. We predict that within this range of fragmentation martens are sensitive to landscape pattern alone, and that landscapes lacking forest interior may not sustain reproducing populations.

The effects of patch size and spatial distribution on forest interior are illustrated using three landscape patterns at the same level of fragmentation, with each landscape having approximately 20% of the area in openings (Fig. 6). The first landscape represents one of our study sites with open areas in a dispersed pattern that has resulted in the loss of much of the forest interior (Fig. 6a). The other images are of two simulated landscapes having 20% openings in which the openings are either clustered (Fig. 6b) or aggregated

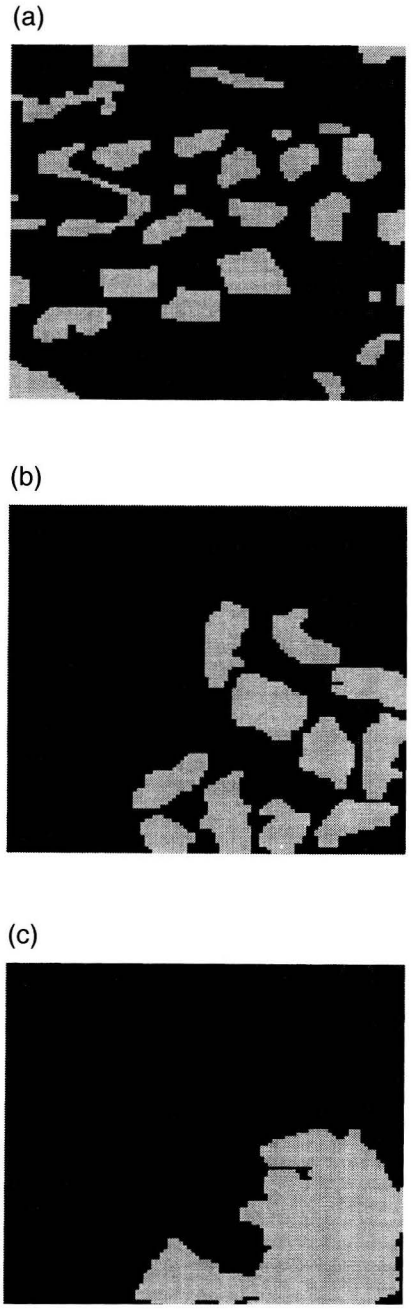


Fig. 6. Three landscape patterns with approximately 20% of the area in openings: (a) an actual landscape in Utah; (b) a simulated landscape with clustered patches; and (c) a simulated landscape with openings aggregated into a single patch to maximize forest interior. Black represents forest and grey represents open areas.

into a single patch (Fig. 6c). The simulations were created with a computer program that places patches on a landscape at any specified proportion and spacing (Hargis, Bissonette & David 1997), using digitized clearcut patch shapes from the Uinta Mountains. The comparison clearly illustrates the greater size of forest interior and fewer disruptions in continuity of habitat that occurs when unsuitable habitat is clustered or occupies a single patch.

Assuming American martens do require forest interior for reproductive habitat, management should consider the guidelines developed by Franklin & Forman (1987) for conservation of forest interior species in managed landscapes. They recommend that timber harvests be undertaken progressively outward from a single patch or in clustered cuts so that disturbance patches are consolidated and larger areas of undisturbed forest could be maintained. For martens, progressive cutting rather than clustered cuts would be preferred, because the forested buffers left between tightly clustered clearcuts have little apparent value to martens, and represent additional loss of habitat rather than useable forest. Progressive cutting from a single patch would create maximum aggregation of disturbance and retain the largest amount of interior forest habitat.

Acknowledgements

This project was carried out within the Utah Cooperative Fish and Wildlife Research Unit (USGS Biological Resources Division). We thank F. Bartlett for logistical support of this project and K. Paulin and other Forest Service employees who provided us with necessary maps and aerial photos. We are indebted to S. Kuerner, H. Sloan, D. Masters, T. Sajwaj, K. Lischak, A. Krawarik, C. Zank, R. Vinkey, P. Lortz and R. Rood for assisting in collecting data under arduous conditions, and to the martens for being there. B. Milne and T. Keitt provided software for calculations of mass fractal dimension. Thanks to S. Brainerd for sending us P. Majewski's translation of Grakov (1972). We also thank P. Bright, S. W. Buskirk, M. Conover, J. David, S. Durham, J. Long, D. Ramsey and M. Ritchie for their helpful review of manuscript drafts. We acknowledge use of the Khoros image processing environment, a trademark of Khoral Research Inc., and FRAGSTATS, a spatial pattern analysis program in the public domain developed by K. McGarigal and B. Marks.

References

Archibald, W.R. & Jessup, R.H. (1984) Population dynamics of the pine marten (*Martes americana*) in the Yukon Territory. *Northern Ecology and Resource Management* (eds R. Olson, R. Hastings & F. Geddes), pp. 81–97. University of Alberta Press, Edmonton, Canada.

Balharry, D. (1993) *Factors affecting the distribution and population density of pine martens* (Martes martes L.) *in Scotland*. PhD Thesis. University of Aberdeen, Aberdeen, UK.

Bartell, S.M. & Brenkert, A.L. (1991) A spatial-temporal model of nitrogen dynamics in a deciduous forest watershed. *Quantitative Methods in Landscape Ecology* (eds M.G. Turner & R.H. Gardner), pp. 379–398. Springer-Verlag, New York, NY.

Bjärvall, A., Nilsson, E. & Norling, L. (1977) The importance of old-growth forest for capercaillie and marten. *Fauna Och Flora*, **72**, 31–38 [in Swedish].

Brainerd, S.M. (1990) The pine marten and forest fragmentation: a review and general hypothesis. *Transactions of the 19th International Congress of Game Biologists* (ed. S. Myrberget), pp. 421–434. Trondheim, Norway.

Brainerd, S.M. (1997) *Habitat selection and range use by the Eurasian pine marten* (Martes martes) *in relation to commercial forestry practices in southern boreal Scandinavia*. PhD Thesis. Agricultural University of Norway, Norway.

Bright, P.W. (1993) Habitat fragmentation – problems and predictions for British mammals. *Mammal Review*, **23**, 101–111.

Brown, J.K. (1974) *Handbook for Inventorying Downed Woody Material*. General Technical Report INT-16. USDA Forest Service, Ogden, UT.

Buskirk, S.W. & MacDonald, S.O. (1984) Seasonal food habits of martens in south-central Alaska. *Canadian Journal of Zoology*, **62**, 944–950.

Buskirk, S.W. & Powell, R.A. (1994) Habitat ecology of fishers and American martens. *Martens, Sables, and Fishers: Biology and Conservation* (eds S.W. Buskirk, A.S. Harestad, M.G. Raphael & R.A. Powell), pp. 283–296. Cornell University Press, Ithaca, NY.

Buskirk, S.W., Forrest, S.C., Raphael, M.G. & Harlow, H.J. (1989) Winter resting site ecology of martens in the central Rocky Mountains. *Journal of Wildlife Management*, **53**, 191–196.

Campbell, T.M. (1979) *Short-term effects of timber harvests on pine marten ecology*. MS Thesis. Colorado State University, Fort Collins, CO.

Chapin, T.G. (1995) *Influence of landscape pattern and forest type on use of habitat by marten in Maine*. MS Thesis. University of Maine, Orono, ME.

Chapin, T.G. & Harrison, D.J. (1998) Influence of landscape pattern on habitat use by American marten in an industrial forest. *Conservation Biology*, **12**, 1327–1338.

Chen, J., Franklin, J.F. & Spies, T.A. (1995) Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications*, **5**, 74–86.

Clark, T.W. & Campbell, T.M. (1979) Population organization and regulatory mechanisms of pine martens in Grand Teton National Park, Wyoming. *Conference on Scientific Research in National Parks, Vol. 1* (ed. R.M. Linn), pp. 293–295. National Park Service Transactions and Proceedings Series 5. National Park Service, Washington, DC.

Corn, J.G. & Raphael, M.G. (1992) Habitat characteristics at marten subnivean access sites. *Journal of Wildlife Management*, **56**, 442–448.

Daniel, T.W. & Sterba, H. (1980) Zur ansprache der bestandesdichte. *Allgemeine Forstzeitung*, **91**, 155–157.

Diamond, J.M. (1975) The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation*, **7**, 129–146.

Drew, G.S. (1995) *Winter habitat selection by American marten* (Martes americana) *in Newfoundland: why old growth?* PhD Thesis. Utah State University, Logan, UT.

Efron, B. & Tibshirani, R.J. (1993) *An Introduction to the Bootstrap*. Chapman & Hall Inc., New York, NY.

Franklin, J.F. & Forman, R.T.T. (1987) Creating landscape

patterns by forest cutting: ecological consequences and principles. *Landscape Ecology*, **1**, 5–18.

Frome, E.L., Kutner, M.H. & Beauchamp, J.J. (1973) Regression analysis of Poisson-distributed data. *Journal of the American Statistical Association*, **68**, 935–940.

Grakov, N.N. (1972) Effect of concentrated clearfellings on the abundance of pine marten (*Martes martes* L.). *Byulleteeń Moskovskogo Obshchestva Ispytatelei Prirody Otdel Biologicheskii*, **77**, 14–23 [in Russian, with English summary].

Gustafson, E.J. & Parker, G.R. (1992) Relationships between landcover proportion and indices of landscape spatial pattern. *Landscape Ecology*, **7**, 101–110.

Hargis, C.D. & Bissonette, J.A. (1997) Effects of forest fragmentation on populations of American marten in the intermountain west. *Martes: Taxonomy, Ecology, Techniques and Management* (eds G. Proulx, H. Bryant & P.M. Woodard), pp. 437–451. Provincial Museum of Alberta, Edmonton, Canada.

Hargis, C.D. & McCullough, D.R. (1984) Winter diet and habitat selection of marten in Yosemite National Park. *Journal of Wildlife Management*, **48**, 140–146.

Hargis, C.D., Bissonette, J.A. & David, J.L. (1997) Understanding measures of landscape pattern. *Wildlife and Landscape Ecology: Effects of Pattern and Scale* (ed. J.A. Bissonette), pp. 231–261. Springer-Verlag, New York, NY.

Harris, L.D. (1984) *The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity*. University of Chicago Press, Chicago, IL.

Hodgman, T.P., Harrison, D.J., Phillips, D.M. & Elowe, K.D. (1997) Survival of American marten in an untrapped forest preserve in Maine. *Martes: Taxonomy, Ecology, Techniques and Management* (eds G. Proulx, H. Bryant & P.M. Woodard), pp. 86–99. Provincial Museum of Alberta, Edmonton, Canada.

Homer, C.G., Ramsey, R.D., Edwards, T.C. Jr & Falconer, A. (1997) Landscape cover-type modeling using a multiscene thematic mapper mosaic. *Photogrammetric Engineering and Remote Sensing*, **63**, 59–67.

van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893–901.

Ims, R.A. (1995) Movement patterns related to spatial structures. *Mosaic Landscapes and Ecological Processes* (eds L. Hansson, L. Fahrig & G. Merriam), pp. 85–109. Chapman & Hall, London, UK.

Katnik, D.D. (1992) *Spatial use, territoriality, and summer–autumn selection of habitat in an intensively harvested population of martens on commercial forestland in Maine*. MS Thesis. University of Maine, Orono, ME.

Katnik, D.D., Harrison, D.J. & Hodgman, T.P. (1994) Spatial relations in a harvested population of martens in Maine. *Journal of Wildlife Management*, **5**, 600–607.

Koehler, G.M. & Hornocker, M.G. (1977) Fire effects on marten habitat in the Selway-Bitterroot Wilderness. *Journal of Wildlife Management*, **41**, 500–505.

Lofroth, E.C. (1993) *Scale dependent analyses of habitat selection by marten in the sub-boreal spruce biogeoclimatic zone, British Columbia*. MS Thesis. Simon Fraser University, British Columbia, Canada.

Lord, J.M. & Norton, D.A. (1990) Scale and the spatial concept of fragmentation. *Conservation Biology*, **4**, 197–202.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Chapman & Hall, New York, NY.

McGarigal, K. & Marks, B.J. (1995) FRAGSTATS: *Spatial Analysis Program for Quantifying Landscape Structure*. General Technical Report PNW-GTR-351. United States Department of Agriculture Forest Service , Portland, OR.

Mills, L.S. (1995) Edge effects and isolation: red-backed voles on forest remnants. *Conservation Biology*, **9**, 395–403.

Milne, B.T. (1991) Lessons from applying fractal models to landscape patterns. *Quantitative Methods in Landscape Ecology* (eds M.G. Turner & R.H. Gardner), pp. 199–235. Springer-Verlag, New York, NY.

Nordstrom, L. (1995) *Small mammal use of forested corridors in fragmented landscapes*. MS Thesis. Washington State University, Pullman, WA.

O'Doherty, E.C., Ruggiero, L.F. & Henry, S.E. (1997) Home-range size and fidelity of American martens in the Rocky Mountains of southern Wyoming. *Martes: Taxonomy, Ecology, Techniques and Management* (eds G. Proulx, H. Bryant & P.M. Woodard), pp. 123–134. Provincial Museum of Alberta, Edmonton, Canada.

O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S.W., Dale, V.H. & Graham, R.L. (1988) Indices of landscape pattern. *Landscape Ecology*, **1**, 153–162.

Potvin, F. & Breton, L. (1997) Short-term effects of clearcutting on martens and their prey in the boreal forest of western Quebec. *Martes: Taxonomy, Ecology, Techniques and Management* (eds G. Proulx, H. Bryant & P.M. Woodard), pp. 452–474. Provincial Museum of Alberta, Edmonton, Canada.

Powell, R.A. (1994) Structure and spacing of *Martes* populations. *Martens, Sables, and Fishers: Biology and Conservation* (eds S.W. Buskirk, A.S. Harestad, M.G. Raphael & R.A. Powell), pp. 101–121. Cornell University Press, Ithaca, NY.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.

Raphael, M.G. (1988) Habitat associations of small mammals in a subalpine forest, southeastern Wyoming. *Management of Amphibians, Reptiles, and Small Mammals in North America* (eds R.C. Szaro, K.E. Severson & D.R. Patton), pp. 359–366. General Technical Report RM-GTR-166. USDA Forest Service, Fort Collins, CO.

Raphael, M.G. & Jones, L.L.C. (1997) Characteristics of resting and denning sites of American martens in central Oregon and western Washington. *Martes: Taxonomy, Ecology, Techniques and Management* (eds G. Proulx, H. Bryant & P.M. Woodard), pp. 146–165. Provincial Museum of Alberta, Edmonton, Canada.

Reineke, L.H. (1933) Perfecting a stand density index for even-aged forests. *Journal of Agricultural Research*, **46**, 627–638.

Ripple, W.J., Bradshaw, G.A. & Spies, T.A. (1991) Measuring forest landscape patterns in the Cascade Range of Oregon, USA. *Biological Conservation*, **57**, 73–88.

Rosenberg, K.V. & Raphael, M.G. (1986) Effects of forest fragmentation on vertebrates in Douglas-fir forests. *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates* (eds J. Verner, M.L. Morrison & C.J. Ralph), pp. 263–272. University of Wisconsin Press, Madison, WI.

Sherburne, S.S. & Bissonette, J.A. (1993) Squirrel middens influence marten use of subnivean access points. *American Midland Naturalist*, **129**, 204–207.

Sherburne, S.S. & Bissonette, J.A. (1994) Marten subnivean access point use: response to subnivean prey levels. *Journal of Wildlife Management*, **58**, 400–405.

Simon, T.L. (1980) *An ecological study of the marten in the Tahoe National Forest, California*. MS Thesis. California State University, Sacramento, CA.Snyder, J.E. & Bissonette, J.A. (1987) Marten use of clear-cuttings and residual forest stands in western Newfoundland. *Canadian Journal of Zoology*, **65**, 169–174.

Soutiere, E.C. (1979) Effects of timber harvesting on marten in Maine. *Journal of Wildlife Management*, **43**, 850–860.

Spencer, W.D., Barrett, R.H. & Zielinski, W.J. (1983) Mar-

ten habitat preferences in the northern Sierra Nevada. *Journal of Wildlife Management*, **47**, 1181–1186.

Spies, T.A., Ripple, W.J. & Bradshaw, G.A. (1994) Dynamics and pattern of a managed coniferous forest landscape in Oregon. *Ecological Applications*, **4**, 555–568.

Steventon, J.D. & Major, J.T. (1982) Marten use of habitat in a commercially clear-cut forest. *Journal of Wildlife Management*, **46**, 175–182.

Taylor, S.L. (1993) *Thermodynamics and energetics of resting site use by the American marten* (Martes americana). MS Thesis. University of Wyoming, Laramie, WY.

Thomas, J.W. (1979) *Wildlife Habitats in Managed Forests: the Blue Mountains of Oregon and Washington*. United States Department of Agriculture Forest Service Agriculture Handbook Number 533. US Government Printing Office, Washington, DC.

Thompson, I.D. (1994) Marten populations in uncut and logged boreal forests in Ontario. *Journal of Wildlife Management*, **58**, 272–279.

Thompson, I.D. & Colgan, P.W. (1994) Marten activity in uncut and logged boreal forests in Ontario. *Journal of Wildlife Management*, **58**, 280–288.

Thompson, I.D. & Harestad, A.S. (1994) Effects of logging on American martens, and models for habitat management. *Martens, Sables, and Fishers: Biology and Conservation* (eds S.W. Buskirk, A.S. Harestad, M.G. Raphael & R.A. Powell), pp. 355–367. Cornell University Press, Ithaca, NY.

Turner, M.G. (1987) *Landscape Heterogeneity and Disturbance*. Springer-Verlag, New York, NY.

Turner, M.G. & Dale, V.H. (1991) Modeling landscape disturbance. *Quantitative Methods in Landscape Ecology* (eds M.G. Turner & R.H. Gardner), pp. 323–352. Springer-Verlag, New York, NY.

Turner, M.G., Gardner, R.H., Dale, V.H. & O'Neill, R.V. (1989) Predicting the spread of disturbance across heterogeneous landscapes. *Oikos*, **55**, 121–129.

Verboom, B. & van Apeldoorn, R. (1990) Effects of habitat fragmentation on the red squirrel *Sciurus vulgaris*. *Landscape Ecology*, **4**, 171–176.

Voss, R.F. (1988) Fractals in natures: from characterization to simulation. *The Science of Fractal Images* (eds H.O. Peitgen & D. Saupe), pp. 21–70. Springer-Verlag, New York, NY.

Wallin, D.O., Swanson, F.J. & Marks, B. (1994) Landscape pattern response to changes in pattern generation rules: land-use legacies in forestry. *Ecological Applications*, **4**, 569–580.

Weckwerth, R.P. & Hawley, V.D. (1962) Marten food habits and population fluctuations in Montana. *Journal of Wildlife Management*, **26**, 55–74.

Whitcomb, R.F., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K. & Bystrak, D. (1981) Effects of forest fragmentation on avifauna of the eastern deciduous forest. *Forest Island Dynamics in Man-Dominated Landscapes* (eds R.L. Burgess & D.M. Sharpe), pp. 125–205. Springer-Verlag, New York, NY.

Wiens, J.A., Stenseth, N.C., Van Horne, B. & Ims, R.A. (1993) Ecological mechanisms and landscape ecology. *Oikos*, **66**, 369–380.

Wilcox, B.A. (1980) Insular ecology and conservation. *Conservation Biology: an Evolutionary-Ecological Perspective* (eds M.E. Soulé & B.A. Wilcox), pp. 95–117. Sinauer Associates, Sunderland, MA.

Received 2 October 1997; revision received 24 November 1998